Introduction

One of the first things that catches the attention of a diver entering the warm waters of the coral reef is the phenomenal diversity, abundance, and beauty of fishes swimming before them. While all organisms on the coral reef are integrated into its overall ecology, fishes are certainly among the more readily observable taxons, and are an extremely important component of overall reef function. No comprehensive survey or community-level study of a coral reef would be complete without fishes being evaluated. Because of their importance, which is reflected by the large volume of literature on their biology, this chapter is devoted entirely to the ecology of coral reef fishes.

Before proceeding further, it seems appropriate that at least a basic introduction to fishes be provided for students who have not had courses in general zoology or introductory ichthyology. First, what is a fish? While that might seem intuitively obvious, the shear evolutionary diversity of fishes, makes defining them somewhat problematical. Nonetheless, a workable definition comes from Nelson (1984) who states, "...fish can be simply defined as aquatic poikilotherm vertebrates that have gills throughout life and limbs, if any, in the shape of fins."

Of vertebrates, fishes account for about half of the approximately 43,000 living species. There are currently about 21,723 living fish species, comprising roughly 445 families placed in 50 orders (Nelson 1984). Of the 21,723 species of fishes, about 58% are marine, 41% live in freshwater, and the remainder (1%) migrate regularly between marine and freshwaters (Cohen 1970).

At the highest taxonomic level of differentiation, living fishes are subdivided into four classes:

| Class               | Common Name              | Approximate Number of Species
<table>
<thead>
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<tbody>
<tr>
<td>Cephalaspidomorphi</td>
<td>lampreys</td>
<td>41</td>
</tr>
<tr>
<td>Myxin</td>
<td>hagfishes</td>
<td>32</td>
</tr>
<tr>
<td>Chondrichthyes</td>
<td>cartilaginous fishes</td>
<td>793</td>
</tr>
<tr>
<td>Osteichthyes</td>
<td>bony fishes</td>
<td>20857</td>
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1 From data provided by Nelson (1984).
The lampreys and hagfishes are living remnants of a much more speciose assemblage of jawless fishes called ostracoderms that flourished in the seas during the Silurian and part of the Devonian (roughly 400-300 million years before the present). These eel-like fishes lack jaws, paired fins, bone, and vertebral column, although they do have a persistent notochord (Nelson 1984). Unlike other fishes, their gills open externally via numerous pores. Lampreys are found in the cold fresh and/or marine waters of higher latitudes, and are most notorious for parasitizing other fishes by sucking their bodily fluids. Hagfishes are found in marine waters less that 13° C, which confines them to temperate seas or to the deep (and cold) bottom of tropical oceans. They occupy soft bottom regions where they forage for small infaunal invertebrates or scavenge on dead organisms.

Fishes of the class Chondrichthyes possess cartilaginous skeletons although teeth, jaws, and vertebral column can be calcified. Other chondrichthyan features include: a skull which lacks sutures; unsegmented soft fin rays; swimbladder or lungs absent; and internal fertilization (Nelson 1984). The class includes the sharks, skates, rays, chimaeras and ratfishes, and is subdivided into six or 13 orders depending upon the author (Nelson 1984 or Compagno 1973, 1977). Distributed world wide, cartilaginous fishes are all carnivorous although feeding habits are diverse, ranging from planktivores to benthonic mollusc/crustacean crushers, to predators that bite large chunks of flesh from their prey. While many species are associated with coral reefs, their behavior and ecology has generally received less attention from investigators than that of bony fishes. This is probably mostly the result of the difficulty associated with studying large mobile fishes like sharks, rays, and skates. Certainly it is not due to any lack of interest from scientists toward the chondrichthyian fishes. Nonetheless, much less is known about them as a group compared to the bony fishes and they will not be treated further in this chapter.

The class Osteichthyes is comprised of fishes which have skeletons, at least in part, with true bone. The group also possesses numerous other features including: a skull with sutures; segmented soft fin rays; a swimbladder or functional lung which is usually, but not always, present; and a preponderance of species utilizing external rather than internal fertilization (Nelson, 1984). The Osteichthyes contains approximately 20,857 species of bony fishes that split into at least four evolutionary lines early in their evolution (Moyle and Cech 1988, Nelson 1984). Those lines are: 1) the lungfishes represented today by six freshwater species living in Africa, South America, and Australia; 2) the crossopterygians represented by a single remaining species, the coelacanth, inhabiting the deep marine waters off eastern Africa; 3) the bichirs, eleven freshwater species found in central Africa; and 4) the ray-finned fishes represented by the remaining 20,839 species of bony fishes.

The ray-finned fishes include sturgeon and paddlefishes (25 species), gars (7
species), bowfin (1 species), and teleosts (20,806 species). Teleosts, which comprise
99.8% of all bony fish species, are commonly referred to as "advanced" bony fishes.
The group contains 35 orders which exhibit remarkable diversity of form and life-style.
Nonetheless, the advanced bony fish fauna is dominated by the fishes of a single
teleost order, the Perciformes. One hundred and fifty of the 445 families listed by
Nelson (1984) are contained within the order Perciformes, and some of those 150 are
the most speciose of fish families [i.e. gobies (Gobiidae) - about 1500 species, wrasses
(Labridae) - about 500 species, sea basses (Serranidae) - 370 species, etc.]. Species
from this order are the dominant component of coral reef fish fauna.

As might be expected, fishes are not uniformly distributed throughout the world's
oceans. About 9800 marine species (78% of all marine species) live along margins of
land masses in waters to about 200 m deep (Moyle and Cech 1988). Somewhere
between 66-89% of those 9800 species (30-40% of all fish species) are found on coral
reefs and associated habitats around the world (Moyle and Cech 1988)! Without
question, coral reefs have by far the highest diversity of ichthyofauna of any marine or
freshwater ecosystem.

Given the diversity of coral reef fishes, high variability between coral reef fish
communities world-wide, and the voluminous literature on the ecology of coral reef
fishes, it is beyond the scope of this chapter to even begin to fully treat the subject of
the biology and ecology of coral reef fishes. While this narrative provides good general
coverage of several important topics relating to the biology of coral reef fishes, it
necessarily lacks depth. For the student who wishes to pursue the subject in greater
detail, an excellent review of coral reef fish ecology is available (Sale 1991a).

Evolution of Coral Reef Fishes

Where did coral reef fishes come from and when did they evolve? For the most
part, to talk about the evolution of coral reef fishes is to talk about the evolution of
perciform fishes since the vast majority of reef fishes are from this order. According
to Carroll (1987) the perciforms arose from beryciform-like acanthopterygian (spiny-rayed)
ancestors during the late Cretaceous some 65-70 million years ago (modern beryciform
fishes include familiar fishes like squirrelfishes, soldierfishes, and beardfishes).
Between the late Cretaceous and the early Tertiary (to about 50 million years before the
present), the perciform fishes underwent a period of rapid evolutionary change (Carroll
1987). Within about 20 million years of the first appearance of perciform fishes, they
achieved a structural complexity and taxonomic diversity that is essentially
indistinguishable from that of living forms (Choat and Bellwood 1991).

The appearance and subsequent rapid evolution of perciform fishes coincides
closely with changes in coral reefs that were occurring at approximately the same time
(Rosen 1988, Choat and Bellwood 1991). While reef-building corals were present long before the late Cretaceous, they were not the scleractinian corals that dominate modern reefs. Scleractinians did not appear in the fossil record until the late Cretaceous/early Tertiary, after a period of decline and extinctions of many earlier coral taxa at the end of the Cretaceous (Fagerstrom 1987). In the early Tertiary, scleractinian corals became the dominant coral taxa and coral reefs, which were predominant features of many shallow tropical seas, took on a modern appearance (Choat and Bellwood 1991). In summary, modern coral reef fishes are an ancient group which evolved some 70-50 million years before the present in conjunction with the evolution of modern coral reefs dominated by scleractinian corals. As such, the biology of both reef corals and fishes is intimately intertwined.

Coral Reef Fishes - Taxa of Major Importance

Approximately 100 families of bony fishes are known to have coral reef representatives (Leis 1991a). Of those, perciform fishes predominate in regard to both species richness and abundance. Of 103 families of reef fishes cataloged from reefs in Micronesia, 51 were perciforms (Myers 1989, Choat and Bellwood 1991). Williams and Hatcher (1983) in their survey of reef fishes from various habitats on the Great Barrier Reef found that perciform fishes were by far the most abundant on the reefs sampled.

Of the 50 or so perciform families associated with coral reefs, just eight families from three major taxa are particularly important in regard to complete association with coral reef environments (Choat and Bellwood 1991, Sale 1991b):

**Labroids**
- Labridae - wrasses
- Scaridae - parrotfishes
- Pomacentridae - damselfishes

**Acanthuroids**
- Acanthuridae - surgeonfishes
- Siganidae - rabbitfishes
- Zanclidae - moorish idols

**Chaetodontoids**
- Chaetodontidae - butterflyfishes
- Pomacanthidae - angelfishes

The vast majority of these fishes have distribution patterns which correspond to the distribution of coral reefs and spend their entire postsettlement life cycle in association with those reefs (only a small percentage of the labroids have invaded...
colder waters of temperate reefs). Within all of these taxonomic groupings there is a tendency for ecologically similar species to form extensive guilds, which in itself, is one of the distinctive elements of coral reef fish faunas (Choat and Bellwood 1991). The fishes of these groupings also have feeding habits which have diverged dramatically from the generalized large-mouthed carnivores from which they evolved. Many are "picker-type" microcarnivores or herbivores which exploit the benthonic biota of coral reefs, while others have adopted planktivory as their primary mode of feeding.

The labroids include the wrasses, the parrotfishes, and the damselfishes. Wrasses are a large family of some 500 carnivorous species which specialize in taking benthonic invertebrates, primarily crustaceans and molluscs (Sano et al. 1984). There are about 68 species of parrotfishes and most are primarily herbivorous. The damselfishes, which total 235 species worldwide, have diets which range from herbivory, to planktivory, to feeding on benthic crustaceans. Many wrasses and parrotfishes exhibit sequential hermaphroditism and have complex social systems. Territorial behavior is common among the damselfishes.

The acanthuroids include the surgeonfishes, rabbitfishes, and moorish idols. There are about 76 surgeonfish species, 25 rabbitfish species, and only one species of moorish idol (included in the surgeonfish family by Nelson 1984). For the most part, fishes of these families are herbivores or detritivores, although some of the surgeonfishes, especially species from the genera Naso and Acanthurus, are planktivores (Choat and Bellwood 1991). Although not as speciose as the labroids and chaetodontoids, their largely herbivorous feeding behavior has profound impact on the ecology of coral reefs, and acanthuroids are often among the most abundant fishes on coral reefs (Choat 1991).

The chaetodontoids include the butterflyfishes and the angelfishes. Both families exhibit marked lateral compression, possess small terminal mouths with bristlelike teeth, and are often among the most brightly colored fishes on the reef. There are some 114 species of butterflyfishes, of which 90% occur in the Indo-Pacific (Allen 1981). Almost half of the butterflyfishes feed on corals, although others feed on small reef invertebrates, algae, or even plankton. There are 74 species of angelfishes, most occurring in the western Pacific (Choat and Bellwood 1991). Angelfishes exhibit three main feeding strategies: consumption of benthonic invertebrates (mainly sponges), herbivory, and plankton feeding (Allen 1981).

Sale (1991b) also points out that there are at least eleven additional families of fishes that can be considered especially important based on a combination of reef association and study by marine ecologists. Those families include: the speciose demersal, site attached blennies (Blenniidae) and gobies (Gobiidae); the small, nocturnally active predatory cardinalfish (Apogonidae) and grunt (Haemulidae) families; the bizarre and highly evolved boxfishes (Ostraciidae), puffers (Tetraodontidae), and

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triggerfishes (Balistidae); the large, often piscivorous, predatory sea basses (Serranidae), snappers (Lutjanidae), and emperors (Lethrinidae); and the frequently-planktivorus squirrelfishes and soldierfishes (Holocentridae).

**Coral Reef Fishes - Zoogeographical Considerations**

The zoogeography of marine fishes is much less well understood in comparison to that of their freshwater counterparts which exhibit patterns of distribution based largely on continental drift (plate tectonics) and the geography of drainage systems. Zoogeographical regions of marine fishes have generally been defined on the basis of fish faunal changes, which themselves seem to correlate to changes in oceanographic conditions relating to current patterns or geographic location. Because of the mobile nature of fishes and the widespread pelagic dispersal of marine fish larvae, zoogeographic boundaries are not clear-cut nor are they rigid in time (Moyle and Cech 1988). As a result, discussions of the zoogeography of marine fishes have been largely descriptive in nature.

An exhaustive, relatively recent, and widely cited treatment of the subject of marine zoogeography is the work of Briggs (1974). Briggs divided tropical oceans into four large regions, based primarily on the distribution of reef fishes. Those regions are: 1) the Indo-Pacific Region, 2) the Eastern Pacific Region, 3) the Western Atlantic Region, and 4) the Eastern Atlantic Region. These regions are separated from each other by continental land masses or vast expanses of deep ocean, and possess northern and southern boundaries which correspond roughly to the 20° C isotherm for the coldest period of the year (Moyle and Cech 1988).

The Indo-Pacific region is by far the largest of Briggs' zoogeographical regions stretching from the east coast of Africa all the way to the Hawaiian Islands, Marquesas, and Easter Island. This region is rich in coral reefs and easily has the highest diversity of reef fishes of any of Briggs' regions. There are probably in excess of 3000 species of shore fishes in the Indo-Pacific, compared to less than 1000 for each of the other regions (Briggs 1974). Many of these 3000+ species are wide-ranging over vast distances within the Indo-Pacific. However, isolated oceanic island chains in the Indo-Pacific region often have a rich endemic fauna. For example, in Hawaii about 30% of the reef fish fauna is endemic, the highest level of endemism for marine fishes in the Indo-Pacific region (Hourigan and Reese, 1987). While most families of coral reef fishes occur in all four of the regions, a few families are endemic to the Indo-Pacific like pegasids (seamoths), sillaginids (smelt-whitings), kraemerids (sand gobies), siganids (rabbitfishes), and plesiopids (roundheads) (Moyle and Cech 1988). Although the Indo-Pacific region shares most of its fish families with other regions, only a small number of species occur in other zoogeographical regions: sixty-two species are shared with the Eastern Pacific, eight species with the Western Atlantic, and 32 species with the
The Eastern Pacific Region extends along the west coast of the New World from the tip of Baja California to the Gulf of Guayquil which lies at approximately 3° south latitude on the west coast of South America. It is separated from the Indo-Pacific by expanses of deep ocean and from the Western Atlantic by the isthmus of Panama and contains some 800+ species of shore fishes (Moyle and Cech 1988). The Western Atlantic Region, home to over 900 species of near shore fishes, includes the eastern coastlines of Mexico and Central America, the east coast of South America to Cape Frio, the tip of Florida, and numerous islands of the West Indies and Bermuda (Moyle and Cech 1988). Coral reefs are well developed in the Western Atlantic Region and much of its fish fauna is associated with those reefs. While ecological roles of fishes on these reefs appear to be similar to those on Indo-Pacific reefs, only eight species are shared by the two regions, and subtle differences in the ecology of their fishes exist. For example, in the Indo-Pacific the principal cleaner fishes are wrasses while in the Western Atlantic, that ecological role is assumed by the gobies (Moyle and Cech 1988). The Eastern Atlantic Region, the smallest and most isolated of the four regions defined by Briggs, extends along the west coast of Africa from Cape Verde to Angola and includes the offshore islands of Cape Verde, St. Helena, and Ascension. This is the most species-poor region, possessing only about 450 species of shore fish. It contains few coral reefs which may help to explain its relatively low richness of fish species. Reflecting the region's relative isolation, about 40% of the fish species are endemic (Moyle and Cech 1988).

In a recent paper, Thresher (1991) reviewed and evaluated literature on geographic variability in the ecology of coral reef fishes. His review includes an evaluation of geographic trends in species and family richness which is relevant to this discussion of coral reef fish zoogeography. Working from species checklists compiled by other workers from twenty-one different warm-water locations in the Indian, Pacific, and Atlantic Oceans, Thresher plotted the number of species and families present at each location against the location's longitude within its respective ocean basin.

For sites within the Pacific Ocean, Thresher found that there was a statistically significant decline in the number of species and families from west to east across the basin. Indian Ocean sites exhibited an opposite, though nonsignificant, trend (an increase from west to east). The observed longitudinal gradients in species and family richness within the Indo-Pacific seem to correlate well with the widely accepted hypothesis that the center of coral reef fish diversity (radiation) is the Philippines-Indo-Malayan region.

In fact, out of the sites analyzed, Thresher found the highest number of species (about 1000) and families (about 50) from reefs located near the western continental margin of the Pacific (Guam, Great Barrier Reef, New Caledonia). New World reefs
Hawaiian reef fish fauna were recently evaluated by Hourigan and Reese (1987) who identified four main evolutionary/zoogeographical characteristics of Hawaiian fishes. First, they share a close affinity with Indo-west Pacific (IWP) fishes. Most fish species found in Hawaii also occur in the IWP (approximately 70%), and most Hawaiian endemics have sibling species in the IWP. Second, the species richness of Hawaiian fishes, and reef fauna in general, is depauperate relative to their IWP counterparts. In the Philippines, located near the center of IWP fish radiation, there may be as many as 2000 species of fishes. Hawaii only has about 680 species; 440 inshore and 240 epipelagic and deeper. Other Hawaiian marine taxa exhibit similarly low species richness: 2500 IWP mollusc species vs 1000 Hawaiian species; 354 IWP echinoderms vs 90 in Hawaii; >53 IWP coral genera vs 15 Hawaiian genera; etc.. Third, Hawaiian reef fishes exhibit the highest degree of endemism at the species level (about 30% endemics) in the IWP region (for marine fauna). Endemism is also high among other Hawaiian marine groups; 18% for algae, 20% for molluscs, 20% for asteroids, and 40% for polychaetes. Fourth, there is a lack of adaptive radiation among the fishes of the Hawaiian Island chain. Most species are found on all islands and there appears to be high genetic similarity from island to island.

Hourigan and Reese (1987) explain the observed characteristics on the basis of an interaction between Hawaii’s geographic isolation and the life-history of most coral reef fishes. The vast majority of marine organisms, including fishes, produce floating eggs or larvae which are dispersed by water currents (reproduction in coral reef fishes will be discussed in more detail in the next section). Once young recruit to a reef, individuals generally remain near where they settle for the balance of their lives.

According to Hourigan and Reese, the low species richness which characterizes Hawaiian reef fishes is reflective of how difficult it is for organisms with this life-history pattern to reach Hawaii. Adults, which technically might be able to swim to Hawaii from other areas (probably the Indo-west Pacific), aren't inclined to attempt such migrations. Eggs or larvae of reef fishes are rarely in the water for more than about 80 days (often far less). This is not nearly long enough for them to reach the remote islands of the Hawaiian chain, which do not have any direct current systems leading to them from the IWP or elsewhere.

Hourigan and Reese also point out that Hawaii’s isolation probably also accounts for its pronounced endemism. Once species do somehow make it to Hawaii (one mechanism, for example, might be by rafting under floating marine debris), they are well
isolated from their parental stock. Little or no gene flow occurs so divergence and ultimately speciation become more likely. However, island-to-island radiation (speciation) has not happened because planktonic larval dispersal does allow gene flow to occur among fish populations within the Hawaiian Island chain. There is therefore less chance for inter-island divergence, and ultimately speciation, to occur.

Features of the Life History of Coral Reef Fishes

The life-cycle of most coral reef fishes can be subdivided into three distinct biological/ecological phases: 1) a pelagic larval phase, 2) a juvenile phase, and 3) an adult phase. During the pelagic phase, eggs and/or larvae float in open water as a component of marine plankton. The juvenile phase begins when the young fishes settle onto the reef in a process referred to as recruitment. Juveniles tend to be secretive and are less likely to be seen than adults. The adult phase is marked by the onset of sexual maturity, and may be accompanied by a transition from juvenile to adult coloration or morphology. For the majority of coral reef fishes, it is the adult phase which has received the most attention, and only relatively recently has the importance of larval, and to a lesser extent juvenile, ecology been recognized (Doherty 1991, Jones 1991, Leis 1991a, Richards 1982, McFarland 1985, Richards and Lindeman 1987).

Although marine bony fishes are taxonomically and ecologically diverse, the overwhelmingly majority of species have life-histories which include a pelagic larval stage. Leis (1991a) summarized reproductive characteristics of 100 families of bony fishes associated with coral reefs. Out of the 100 evaluated, only four families had life-cycles with no pelagic stage (Plotosidae-eeltail catfishes, Batrachoididae-toadfishes, Pholidichthyidae-the convict blenny, and Sciaenidae-drums/croakers). Leis also noted that one damselfish species, *Acanthochromis polyacanthus*, was reported to lack a pelagic larval stage (Robertson 1973).

Thresher (1991) recognized the two most common spawning modes for coral reef fishes as being: 1) pelagic spawning in which buoyant eggs are shed directly into the water column where they disperse and ultimately hatch into larvae; and 2) demersal spawning in which negatively-buoyant adhesive eggs are tended (usually) by one or both parents until they hatch into larvae which then undergo a planktonic phase. In addition, some coral reef fishes brood their eggs orally or in body pouches, are live-bearers, or produce semi-pelagic eggs with tendrils that may attach them to objects or join them in free-floating clumps (Leis 1991a, Hourigan and Reese 1987, Nelson 1984, Moyle and Cech 1988). The life cycles of coral reef fishes are summarized in Figure F1.

The pelagic larval stage predominates regardless of the spawning mode. Of the
96 families of coral reef fishes listed by Leis (1991a) with a pelagic larval phase, 57 were pelagic spawners (i.e. wrasses, parrotfishes, surgeonfishes, snappers, goatfishes, butterflyfishes, moray eels, etc.), 14 were demersal spawners (i.e. damselfishes, triggerfishes, gobies, blennies, puffers, etc.), two were live-bearers (viviparous brotulas and clinids), six were brooders (ghost pipefishes, and pipefishes and seahorses in body pouches; mouthbrooding cardinalfishes, jawfishes, basslets, and sand stargazers), three produced semi-pelagic eggs (halfbeaks, needlefishes, and silversides), four exhibited more than one type of reproductive mode (herrings, frogfishes, roundheads, and labrisomids) and 10 have an unknown reproductive mode.

The study of pelagic larvae is difficult for several reasons. First, there are the obvious logistic problems associated with accessing and collecting planktonic fish larvae far from shore. Second, the pelagic larvae of reef fishes are difficult to identify to species or even genus for several reasons (Leis 1991a). They are usually very small which makes them difficult to work with. They are not fully developed at hatching and hence pass through many different developmental stages prior to settlement. They often have morphological features as larvae, like fin or cranial spines exceeding the total head-to-tail length of the larva, which are lost when they recruit to the reef.

In spite of these difficulties, information is becoming increasingly available on the natural history and ecology of pelagic reef fish larvae. The length of time that larvae spend as constituents of the plankton is dependent upon species and probably highly variable within each species (Leis 1991a). Furthermore, the length of the pelagic stage may vary geographically or seasonally (Randall 1961, Victor 1986a). Hourigan and Reese (1987) compiled estimates of larval duration for nine families of Indo-west Pacific reef fishes based on analyses of daily growth increments on otoliths by other workers (Brothers et al 1983, Brothers and Thresher 1985). Means ranged from a maximum of about 75 days for the pelagic spawning moray eels to a minimum of 20 days for the mouth-brooding cardinal fishes. The pelagic phase probably ranges from 9 to well in excess of 100 days (Leis 1991a; Brothers and Thresher 1985; Victor 1991, 1986a,b, 1987; Thresher et al. 1989), while the majority of reef fishes appear to have pelagic larval dispersal times of 20-30 days (Victor 1991).

During the pelagic phase, most tropical shorefish larvae appear to feed on other zooplankton including copepods, tintinnids, nauplii, mollusc larvae, larvaceans, chaetognaths, rotifers, and other fish larvae (Randall 1961, Watson 1974, Liew 1983, Jenkins et al. 1984, Houde and Lovdal 1984, Schmitt 1986, Finucane et al. 1991, Leis 1991a). The data available suggest that tropical shorefish larvae have high dietary specificity and that the arrays of items consumed shift with ontogenetic change (Leis 1991a). Most larvae appear to feed mostly during daylight hours, although some may feed more at night (Leis 1991a). Existing data do not support the hypothesis that starvation is a major cause of mortality of reef fish larvae in the purportedly "food-scarce" waters of tropical seas (Doherty et al 1985). A high percent of larvae examined
in feeding studies have food items in their gut, although as Leis (1991a) points out, it is possible that starving larvae may disappear quickly as a result of increased predation.

The pelagic larvae of reef fishes are by no means homogeneously distributed throughout their range, but instead exhibit pronounced heterogeneity both horizontally and vertically. Gray (1993) collected larval fishes along a series of transects running perpendicular to shore between the 30 m and 100 m depth contours off central New South Wales, Australia. Collections were made at the surface and at 20-30 m of depth at three locations along each transect (over the 30, 70, and 100 m depth contours). He found heterogeneity to exist in the horizontal and vertical distributions of many taxa, with horizontal distributional differences being apparent in the inshore-offshore direction (i.e. correlated to bottom depth) rather than longshore. Of 35 families evaluated, seven were more abundant inshore, four were more abundant offshore, and 24 exhibited no horizontal trend.

Across all transects, Gray reported that more taxa and individuals were caught at depth relative to the surface. Twenty families were more numerous at depth, four were most abundant at the surface, and 11 showed no clear distributional pattern by depth. Leis (1991b), in an analysis of the vertical distribution of fish larvae in the Great Barrier Reef Lagoon, found taxon-specific patterns of vertical distribution for 50 fish taxa which were similar overall to those reported by Gray. Most taxa had highest concentrations in the lower portions of the water column (13-20 m) with far fewer being more abundant near the surface (0-6 m) or at mid-depths (6-13 m). Leis reported that the vertical distribution of fish larvae, which was highly structured during the day, was with few exceptions nearly unstructured at night.

Gray (1993) found ontogenetic differences in the distributions of some larvae. For example, the mean size of a larval goatfish (*Liza argentea*, Mugilidae) was greater offshore than inshore and greater at the surface than at depth. Conversely, a larval jack (*Pseudocaranx dentex*, Carangidae) was more abundant at depth than at the surface. Leis (1991b) reported vertical distributions which changed little ontogenetically.


After a period of pelagic development, larvae recruit to the reef environment. Overall, size at settlement ranges broadly, although within a family, settlement sizes of various species can be very similar (Victor 1991). On the smaller end, Victor (1991) recorded a mean standard length (SL) of about 4 mm for settling reef cubbyu drum.
Pareques acuminatus, while Lachner and Karnella (1980) reported sizes at settlement of about 8 mm SL for the goby Eviota epiphanes. On the large extreme, Victor (1991) reports collecting mature pearlfish larvae (Carapus sp.) as large as 174 mm SL, and Leis (1978) recorded settlement lengths of almost 200 mm SL for the porcupinefish Diodon hystrix. Victor (1991) concludes that the majority of reef species settle between 7 and 12 mm SL.

Settlement size as a percentage of size at sexual maturity and maximum size is also quite variable. In the goby Eviota epiphanes, settlement size represents about 80% of size at sexual maturity or 50% of maximum size, which is at the upper end of settlement size for reef fishes (Leis 1991a). Conversely, at the lower end, Bellwood and Choat (1989) report settlement size in parrotfishes to be between 8-20% of size at sexual maturity and 2-10% of maximum size.

How reef fishes move from the pelagic environment to the reef when they are ready to settle is still not well understood. Unless they recruit to the reef, they will be unable to complete their life cycle. Until relatively recently, the most widely held view was that recruitment of fishes to the reef is a passive process in which new recruits are dependent solely upon currents to deposit them onto the reef (Sale 1970). However, most reef fishes are capable swimmers by the end of their pelagic phase, and it is likely that behavior (i.e. swimming) plays a role in their finding suitable habitat (i.e. a reef) in which to settle (Leis 1982, 1991a). Nonetheless, it is unlikely that swimming in and of itself, can account for the movement of fishes over the vast distances (sometimes hundreds of kilometers) necessary to find a suitable reef.

A number of physical mechanisms, summarized by Leis (1991a), have been proposed which could assist fish larvae in returning to coral reef environments. Those processes include: 1) mesoscale current eddies caused by flow around reefs or islands which might return larvae to the reef [this process has been proposed by Lobel and Robinson (1985, 1986) as being an important mechanism by which larvae from the leeward coast of the Big Island are returned to coastal reefs]; 2) tides which may induce eddies near points or banks, or tidal jets through narrow reef passes, both of which could result in reefward transport of larval fishes; 3) internal waves along density discontinuities (a thermocline) which could transport planktonic organisms shoreward; 4) localized upwelling on the leeward side of reefs which might transport deeper-living larvae to the surface close to shore; 5) wind-driven surface layers on the windward sides of reefs might provide a mechanism by which shallow-living larvae could return to the reef; 6) Ekman transport within the top 100 meters could carry larvae toward shore depending upon the position of the reef and the prevailing winds; 7) density-driven shoreward flow of larvae living near the surface and the bottom might occur when water column stratification breaks down nearshore due to wave turbulence but persists offshore; and 8) Stokes transport (small net water movement in the direction of wave propagation when water depth is less than swell wavelength) which could transport
surface-living larvae toward the reef.

Why is a pelagic larval stage so ubiquitous in the life-cycles of coral reef fishes (among marine fishes in general)? Unfortunately, there is no simple clear-cut answer to this question. A pelagic stage is almost certainly the only effective dispersal mechanism available to most coral reef fishes. Sale (1980a) reports that juvenile and adult reef fishes are strongly site attached and sedentary, and are hence relatively ineffectual in regard to dispersal. Conversely, the pelagic larval phase may permit coral reef fishes to disperse on a scale from meters to perhaps thousands of kilometers (Leis 1991a).

While dispersal may be the proximal reason for the widespread occurrence of pelagic larvae, the ultimate reason why dispersal is advantageous remains uncertain. In a system structured by competition for limited resources, dispersal of juveniles away from competitively dominant adults might confer selective advantage to new recruits, assuming that juveniles can locate vacant habitat which is suitable for survival. However, a great deal of evidence suggests that the community structure of coral reef fishes is rarely determined by competition for limiting resources (Ebeling and Hixon 1991; Talbot et al 1978; Hixon 1991, 1993; Sale 1977, 1980a, 1980b, 1991c; Victor 1983, 1991; Doherty and Williams 1988; Doherty 1991) which undermines the concept of dispersal as a competition reducing adaptation (factors determining the community structure of coral reef fishes will be explored in more detail later in this chapter).

It has been hypothesized that coral reefs are patchy, unpredictable environments (Barlow 1981; Sale 1977, 1980a, 1980b, 1991c), and that pelagic dispersal of reef fishes is adaptive in regard to locating patches of available habitat (Barlow 1981). In essence, the reproductive output of adult fish is spread widely via pelagic dispersal. Most offspring will not happen upon suitable habitat and will perish, but some will recruit successfully. This idea of "risk spreading" has merits but there are problems with it and its validity remains to be determined (Leis 1991a).

A number of alternate hypotheses have been postulated to account for the prevalence of pelagic larvae in reef fishes. Pelagic dispersal away from reefs may be an evolutionary response to intense predation pressure on coral reefs (Johannes 1978); predation pressure which exceeds even that of the planktonic environment (see below). It has also been proposed that the pelagic stage is an energy saving mechanism because drifting in slow ocean currents should require less energy than swimming to maintain position over the reef where currents are strong (Bourret et al 1979 as cited by Leis 1991a). It has even been suggested that the pelagic stage keeps larval fishes away from the surf zone where they could be pulverized by waves (Bakun 1986).

Whatever advantage is conferred by the pelagic larval phase, it must outweigh the losses suffered by larvae from planktonic predation and expatriation (i.e. loss to the open ocean or unsuitable coastal habitat). Mortality during the planktonic stage may
approach 100%, much of it attributable to predation by other constituents of the plankton and adult fishes (Hunter 1984, Leis 1991a). Coupled with this high planktonic mortality is the tendency of marine bony fishes to produce great quantities of eggs/larvae. Sale (1980a) in reviewing data on fecundity of coral reef fishes, reports estimates of annual egg production ranging from about 8000 (a damselfish) to over 1,000,000 (a rabbitfish). In spite of high fecundities, adult population sizes may be determined more by what happens in the plankton than by post-recruitment processes like competition or predation on adults and juveniles. However, this is by no means certain and the factors which structure coral reef fish communities remain controversial. Again, this will be discussed further later in this chapter.

Trophic Ecology of Coral Reef Fishes

Understanding the trophic ecology of coral reef fishes is important for many reasons. Most obviously, fishes must eat to survive, and ascertaining what they eat is therefor relevant to understanding their overall biology. Feeding by fishes can have profound impact on the reef community as a whole. When dietary arrays of multi-species assemblages of reef fishes are evaluated, the data provide an insight into energy flow through the coral reef community. Species that feed offshore but return to the reef to defecate (or be consumed by other organisms) import energy to the reef. Species that maintain feeding territories often exclude other fishes (or even some invertebrate species) and hence influence the distribution of species over the reef. Some species are mechanically destructive to the reef substratum when they feed and hence are significant contributors to bioerosion on the reef.

Clearly, the tropic ecology of reef fishes is important and merits consideration. What follows is divided into three sub-sections: herbivores, planktivores, and carnivores. While some of these subdivisions may appear artificial from a purely trophic perspective (i.e. piscine "planktivores" consume zooplankton and are hence "carnivores"), they represent the major functional feeding groups within the fishes. A section entitled "detritivores" was omitted due to a general lack of information on the importance of detritivory in the trophic ecology of coral reef fishes.

Herbivores

Herbivory has not widely evolved in fishes. Given the fact that plant material is abundant in shallow reef environments, the relatively low percentage of herbivorous fishes to have evolved might, on the surface, seem paradoxical. However, extraction of energy from plant material is very difficult for animals due largely to the indigestibility of cellulose and the generally low protein content of most plants (Bowen 1979, Mattson 1980). The majority of fishes have remained carnivorous, most frequently consuming prey by swallowing it whole (Schaeffer and Rosen 1961). The herbivorous fishes which
have evolved utilize innovative mechanisms for processing and assimilating plant material (see Horn 1989).

Marine herbivorous fishes are not uniformly distributed throughout the marine realm, with species richness declining from tropical to temperate regions (Horn 1989). On temperate and boreal reefs, there are relatively few herbivorous fish species, they are generally uncommon, and they consume only a small proportion of the reef’s primary production (Horn 1989). Dominant cold water herbivorous taxa are invertebrates like echinoids, gastropods, and crustaceans (Choat 1991). On coral reefs the situation is quite different.

Herbivorous fishes of coral reefs are among the most abundant and widespread groups of vertebrate herbivores (Choat 1991). Herbivorous fishes on coral reefs account for a large portion of the plant biomass which is removed and their effect on reef algae and ecology is profound (Hay 1991). In fact, the groups of herbivorous fishes that are found on coral reefs are pretty much unique to those ecosystems, not extending beyond the boundaries of coral reefs (Horn 1989). Their seemingly obligate association with coral reefs is sufficiently specific as to define biogeographic boundaries (Gaines and Lubchenco 1982, Choat 1991).

Choat (1991) points out that herbivorous fishes have been implicated in three fundamental processes on coral reefs. First, herbivores provide a link for the flow of energy between primary producers and the reef’s remaining consumers (i.e. carnivorous trophic levels). Second, they influence the distribution, size, internal composition (see Hay 1991), and even rate of production of plants on the reef. Finally, interactions among territorial herbivorous fishes have been instrumental in the development of demographic and behavioral models for reef fishes in general.

Although there are numerous families of coral reef fishes with herbivorous representatives, most appear to be from just four fairly speciose families: Acanthuridae - approximately 76 species, Siganidae - about 25 species, Scaridae - about 79 species, and Pomacentridae - approximately 159 omnivorous or herbivorous species (Choat 1991). Another potentially significant group of herbivores are the blennies (Blenniidae), although they need more study before their importance can be ascertained (Choat 1991).

There is a significant longitudinal trend in the distribution of herbivorous fishes from the four families listed above. According to Choat (1991) most species occur in the Indo-West Pacific region (258 species) where they are the dominant herbivorous group. Species richness drops off markedly on the Pacific Plate (99-105 species), the Eastern Pacific (25 species), the Caribbean (29 species), and the East Atlantic (10 species). On coral reefs outside the Indo-west Pacific, the relative ecological impact of herbivorous fishes may be shared with other groups (Sale 1980a). For example, in the
Caribbean, echinoids and fishes are both important herbivorous taxa (Carpenter 1986).

Herbivorous fishes have characteristic structural features related to their trophic life-style (Choat 1991). Like many percoid fishes, they are deep-bodied with marked lateral compression, a body form thought in part to facilitate maneuverability in the complex relief of a reef environment. The bones and associated muscles supporting the pectoral fins are well developed, and the pelvic fins are thoracic (i.e. located immediately below the pectoral fins). The pectoral fins are frequently used for locomotion and orientation during feeding (Choat 1991). The thoracic placement of the pelvic fins facilitates hydrodynamic stability during deceleration caused by extension of pectoral fins (Marshall, 1965).

In general, the mouths of herbivorous fishes are small and terminal in location. During feeding, pronounced expansion of the oral cavity does not occur, in contrast to carnivorous fishes which frequently expand the oral cavity as they open their mouths to suck in prey (Choat 1991). The teeth of herbivorous fishes tend to be small and incisor-like, are frequently fused in some fashion, and may even form beak-like structures as in the parrotfishes (Choat 1991).

Herbivores have been grouped, according to their potential impact on the algae they consume, into three functional groups: 1) scraping herbivores, 2) denuding herbivores, and 3) non-denuding herbivores (Steneck 1988). Scraping herbivores, like parrotfishes and certain urchins (Diadema), have the greatest impact on algal abundance and also feed on the widest array of algal species. Denuding herbivores, like rabbitfishes and surgeonfishes, can significantly reduce algal biomass when they occur in high densities. Fishes of this group cannot feed on crustose coralline algae and have limited abilities to forage on articulated corallines or leathery macroalgae (Steneck 1988). Non-denuding herbivores, like most damselfishes, exhibit limited ability to significantly reduce algal biomass.

Processing of ingested algae (i.e. crushing of cell walls) is not done by the teeth. Instead other internal structures are used like the well-developed pharyngeal plates of labroids (Scaridae and Pomacentridae) or gizzard-like structures in the alimentary canal of acanthuroids (Acanthuridae and Siganidae). Energy is probably extracted from algae by a number of mechanisms including mechanical trituration, acid digestion, and probably microbial fermentation (Lobel 1981, Rimmer and Wiebe 1987, Choat 1991).

Unfortunately, there is limited information available on the importance of endosymbionts in digestion of plant material by fishes (Choat 1991). Among suggested criteria for utilization of endosymbionts are constant food supply and a slow transit time through the gut to facilitate microbial reproduction (Horn 1989). Not all coral reef herbivores meet these criteria. Surgeonfishes, for example, have gut transit times of only two to four hours (Choat 1991). Yet there is evidence that surgeonfish alimentary

Herbivorous fish foraging is generally marked by continuous rapid grazing over small areas of reef substratum. The most likely targets of this grazing activity are algal turfs and mats, and accumulated organic material (Russ and St. John 1988). The most abundant algal material on reefs are multi-species turfs less that 10 mm in height composed primarily of diminutive filamentous species (Scott and Russ 1987, Steneck 1988, Choat 1991). These turfs also harbor benthonic diatoms, bacteria, and organic detritus. Crustose algae are also present, usually growing on exposed substratum (Littler and Littler 1984; Steneck 1982, 1988; Choat 1991). Algal thalli greater than 10 mm in height ("macroalgae") are relatively rare on reefs (Lewis 1986, Choat 1991). Other potential sources of energy for herbivorous coral reef fishes include algal mats growing on sand and rubble, sea grasses, symbiotic algae associated with sessile invertebrates, and perhaps organic detritus (Choat 1991).

Herbivore grazing is most intense on coral reefs in shallow areas between about 1-5 meters of depth, with grazing intensity exhibiting a relatively linear decline with increasing depth (Steneck 1988). In areas of intense grazing, algal biomass is low and dominated by turfs and crustose coralline algae (Scott and Russ 1987, Steneck 1988, Choat 1991). Despite the low algal biomass present on most coral reefs, the extremely high growth rates of many algae species make shallow coral reefs among the most productive habitats on earth, with much of this productivity being consumed by herbivorous fishes (Hay 1991). On intensely grazed areas (i.e. shallow fore reefs) fishes may take up to 156,000 feeding bites/m²/day and consume from 50-100% of the total algal production (Hay 1991).

Algal biomass is often greatest at or just above MLW where herbivory is low and exhibits a secondary biomass peak at depths greater than 30 m (Earle 1972, Steneck 1988). In areas experiencing reduced herbivory due to strong wave action, experimental exclusion of herbivores, or heavy fishing of herbivores, algal biomass increases and more macroalgae are present (Steneck 1988). In essence, with increased grazing from scraping and denuding herbivores, algal biomass decreases, and algal groups shift from macroalgae, to turfs, and finally to crustose coralline algae (Steneck 1988).

Reef algae have evolved a number defensive "strategies" which enable them to coexist with herbivores. Steneck (1988) describes three basic defensive strategies which are exhibited by algae. The first is resistance to consumption by being structurally difficult to eat. This is the fundamental strategy of the coralline algae. The
second is recovery after being partially consumed and is characteristic of algae capable of rapid growth and regeneration. This is a primary strategy for multi-species turfs. The third strategy is deterrence against being consumed by being unpalatable. Many algae, especially fleshy macroalgae, retain noxious or toxic chemical compounds (secondary metabolites) in their tissues so that herbivores learn to avoid them. These three strategies are not mutually exclusive and many algae species may use more than one to deter herbivores (Steneck 1988, Hay 1991).

A significant physical effect of herbivory by reef fishes is bioerosion which is the degradation of the reef matrix by biological processes (Choat 1991). Both parrotfishes and surgeonfishes have been identified as major bioeroders and sediment producers on coral reefs (Horn 1989, Hutchings 1986). During the grazing process, reef matrix or living coral is scraped up or excavated by foraging fish. These materials are reduced to sediment which is passed through the alimentary tract and redistributed over the reef surface via defecation (Choat 1991). Bioerosion from grazing herbivorous fishes may be an important agent of structural change on coral reefs (Choat 1991).


**Planktivores**

The majority of marine fishes consume plankton during their juvenile phase, although most of these shift to other types of food as they mature (Leis 1991a). However, on coral reefs adult fishes adapted for feeding on zooplankton are quite common and are of major importance to the trophic economy of the coral reef community (Hobson 1991). Coral reefs have adult planktivorous fishes which are active during both day and night, although each period has its own array of species. Virtually every major acanthopterygian (spiny rayed fishes) family present on coral reefs includes species specialized as planktivores (Hobson 1991). However, some families have many species adapted for planktivory. For example, there are many diurnal planktivores among the sea basses (Serranidae), the butterflyfishes (Chaetodontidae), the damselfishes (Pomacentridae), and the trigger/file fishes (Balistidae), while there are many nocturnal planktivores among the squirrel/soldierfishes (Holocentridae), the big-eyes (Priacanthidae), and the cardinalfishes (Apogonidae) (Starck and Davis 1966; Randall 1967; Hobson 1974, 1991). Day-active and night-active planktivores are generally quite dissimilar, not only taxonomically, but both structurally and behaviorally (Hobson 1991). Diurnal and nocturnal planktivores are compared below, beginning with diurnal planktivores.

Diurnal planktivores have diverged much from the generalized, large-mouthed carnivorous ancestors hypothesized for teleost fishes by Schaeffer and Rosen (1961).
and Gosline (1971). In general, diurnal planktivores possess small, upturned mouths, with highly protrusile, though toothless jaws (Davis and Birdsong 1973, Hobson 1991). The oblique positioning of the mouth, which shortens the snout, appears to place both eyes in a position to focus simultaneously on prey giving them the depth perception of binocular vision (Hobson 1991). Coupled with mouth adaptations, are closely spaced, long gill rakers which prevent small ingested prey from escaping through the gill openings. In essence, diurnal planktivores are adapted to target individual zooplankters which are then either sucked in or engulfed by the jaws (Hobson 1991).

The diet of diurnal planktivorous fishes consists primarily of small swimming crustaceans, especially calanoid and cyclopoid copepods (Hobson and Chess 1978, Hobson 1991). Zooplankters taken by reef fishes during the day tend to be transparent due to reduced pigment concentrations and are virtually all less than 3 mm in their greatest dimension, with many being <1 mm maximum dimension (Hobson 1991). A large proportion of the zooplankton that are consumed by diurnal planktivores are "transient" individuals from the open ocean which are carried to the reef by currents (Hobson 1991).

Because diurnal planktivores consume large quantities of open ocean plankton, it has long been postulated that planktivorous fishes are a major trophic link between the coral reef and the open sea (Emery 1968, Davis and Birdsong 1973). There are at least three ways in which energy captured by planktivorous fishes might find its way to other elements of the coral reef community. First, some planktivores may be consumed by larger piscivorous fishes (Choat 1968, Hartline et al. 1972, Polovina 1984). A second, and probably the major path of energy flow from diurnal planktivores to other reef organisms is through their feces (Hobson 1991). Feeding planktivores produce large amounts of feces (sometimes containing largely undigested zooplankton) which "rain down" upon the reef and are consumed by other fishes as well as benthonic herbivores and detritivores (Hobson 1991, Robertson 1982). Also, a temperate zone diurnal planktivorous pomacentrid (Chromis punctipinnis) has been reported to defecate in nocturnal shelters on the reef in southern California, with fecal matter accounting for the importation of about 8 grams of carbon per square meter per year in that environment (Bray et al. 1981). Bray and his colleagues hypothesize that this form of energy importation to the benthos is likely to be even more significant on tropical coral reefs where diurnal planktivores are common and shelter on the reef at night. A third way in which diurnal planktivores may transfer energy to the reef is through death (attributable to sickness or senescence) and subsequent decay.

Although the mouth structure of diurnal planktivores exhibits a high degree of convergence, body shape can be quite different among the various species, and frequently correlates to where a particular species forages on the reef. Most diurnal planktivores maintain station over a section of reef and simply consume individual zooplankters as they drift by with the current. Many unrelated diurnal planktivores
possess streamlined bodies and forked caudal fins which are adaptations which enhance swimming speed (Norman and Greenwood 1963). The degree of streamlining and forking increases in species that forage successively farther from the reef (Hobson 1991). The streamlining helps these species maintain station in the stronger currents which flow along the outer edge of the reef and also enables them to rapidly flee to the safety of the reef at the approach of a potential predator (Hobson 1991).

Not all diurnal planktivores exhibit bodies which are more streamlined than their benthic relatives. Some pomacentrid planktivores (Dascyllus spp. and Amblyglyphidodon spp.) are deeper-bodied and have longer spines than their benthonic relatives (Hobson and Chess 1978). In addition, planktivorous chaetodontids and pomacanthids (angelfishes) are as deep bodied as their benthonic counterparts (Hobson and Chave 1990). Although this body form is probably not as suitable as a streamlined body in regard to maintaining station in strong currents, it is likely to be an effective deterrent to predators because of the tendency of deep-bodied fishes to lodge in the mouth or pharynx of fishes that attempt to swallow them (Hobson 1991).

Planktivorous fishes also exhibit a tendency to be distributed on the basis of size, with larger individuals characteristically feeding close to the reef edge (Hobson 1991). Hobson (1974) in his study of feeding by fishes on the coral reefs off Kona, Hawaii found that the larger species (>10 cm SL) of planktivores were more common near the drop-off at a depth of about 25 meters. Citing that work, Hobson (1991) lists those species as Chaetodon miliaris, Hemitaurichthys polylepis, Chromis verater, Acanthurus thompsoni, Naso hexacanthus, and Xanthichthys auromarginatus. These species were scarce in the waters above the shallower inner reef, while smaller planktivores like Chromis agilis and C. hanui (approximately 7 cm SL maximum size), though numerous at the drop-off, were also abundant in shallower water. In summary, at the reef drop-off there were 12 species of diurnal planktivore constituting 45% of the fishes counted, while over the inner reef there were only 6 planktivorous species comprising just 14.6% of the fishes counted (Hobson 1991).

Hobson and Chess (1978, 1986) reported similar size-related distributions for diurnal planktivores in the waters off Enewetak atoll. At Enewetak, plankton prey size correlated to feeding location, with fishes feeding in deeper water (larger fishes) taking larger zooplankters (2.5-3.0 mm maximum dimension), and fishes feeding in shallower waters (smaller fishes) taking smaller arrays of zooplankton (about 1.0 mm maximum dimension).

Diurnal planktivorous fishes commonly form aggregations when they are feeding in open water (Hobson 1991). It has long been recognized that aggregation may afford fishes some defense against predators (Hobson 1968, Hamilton 1971, Shaw 1978). Hobson (1991) reports that if approached by a large piscivore (i.e. Caranx spp.), aggregations of diurnal planktivores rapidly condense and often swim rapidly toward the
In addition to forming aggregations as an anti-predatory adaptation, diurnal planktivores modify their position in the water-column in response to light. Fishes in the water-column become increasingly susceptible to successful attack by larger piscivorous fishes as ambient light intensity drops (Hobson 1972). Diurnal planktivores respond by foraging closer to the bottom when the sky is overcast compared to bright sunlight, and on clear days will briefly descend toward the bottom when clouds pass in front of the sun (Hobson 1991). In fact, at dawn and dusk there is a complete changeover between the diurnal and nocturnal fish faunas on coral reefs which is light-intensity mediated, highly structured, and ultimately in response to the threat of predation by piscivorous fishes (Hobson 1972). This will be discussed further at the end of the next subsection.

Nocturnal planktivorous fishes have experienced markedly different selection pressures compared to their diurnal counterparts and as a result are really quite different in body morphology, diet, and their distribution over the reef. The fundamental problem facing nocturnal planktivores is visual location of small prey in the dim light of night (Hobson 1991). Almost universally, they have exceptionally large and sensitive eyes as is evidenced by the soldierfishes, the big-eyes, and the cardinalfishes. However, in increasing visual sensitivity, nocturnal fishes have sacrificed some acuity (the ability to resolve images) and, relative to diurnal planktivores, are probably limited in their ability to resolve smaller objects (Munz and McFarland 1973, McFarland 1991, Hobson 1991). In conjunction with the inability to resolve smaller objects, nocturnal planktivores have not evolved the small mouths and binocular vision used by diurnal planktivores to select and engulf individual small zooplankters. Instead, their mouths are relatively large and terminal, having diverged little from the generalized, large-mouthed carnivorous ancestors hypothesized for teleost fishes by Schaeffer and Rosen (1961) and Gosline (1971).

The diet of nocturnal planktivorous fishes consists primarily of relatively large zooplankton (>2 mm maximum dimension), which are taken not so much as a result of preference for larger prey, but rather because of the inability of these fishes to see and therefore consume smaller zooplankton species (Hobson 1991). As a result of visual limitations, small open-ocean zooplankton which comprise the major prey of diurnal planktivores and which are actually more abundant at night compared to day, are essentially absent from the diets of nocturnal planktivores (Hobson and Chess 1978, 1986; Hobson 1991). Planktonic prey that are taken by nocturnal planktivores include semipelagic residents of the reef which rise into the water column during the night, larger holoplanktonic residents like mysids, and some large open-ocean plankton like euphausids (Hobson 1974, Hobson and Chess 1978, Gladfelter 1979). Many of the resident zooplankton, in addition to larger size, are opaque or awkward swimmers which makes them appropriate targets in the dim nocturnal light (Hobson 1991).
Nocturnal planktivores that consume resident zooplankton are not, like their diurnal counterparts, a major trophic link between the open ocean and coral reef community. However, not all nocturnal planktivorous fishes feed exclusively over the coral reef, and within a particular species, some individuals may leave the reef to feed offshore. For example, Hobson (1991) reports that some Priacanthus cruentatus, Myripristis murdjan, and M. amaenus from Hawaiian reefs migrate seaward at night to feed on larger open-ocean zooplankton and other pelagic organisms like cephalopods. Those individuals, of course, do represent a direct trophic link between the open-ocean and the coral reef. Hobson (1991) maintains that, unlike diurnal planktivores, the feces of nocturnal planktivores are probably not the primary way that energy is passed on to other segments of the reef. Feces are hard to see at night, which probably limits coprophagy by other fishes. Also, nocturnal planktivores take larger and fewer prey, digestion is slower, and defecation less frequent. Finally, nocturnal planktivores do not aggregate like their diurnal counterparts which greatly facilitates coprophagy during the day. The flow of energy from nocturnal planktivores to other elements of the coral reef community may go primarily through piscivorous predators (Hobson 1991).

Nocturnal planktivores are more widely dispersed over the reef than diurnal planktivores. At dusk, they leave shelter sites (holes, crevices, caves, etc) to feed nearby or migrate to feeding areas elsewhere (Hobson 1972). They do not appear to form aggregations which are so characteristic of diurnal species, instead dispersing to forage individually or in small, loosely associated groups (Hobson 1991). Their nocturnal prey, rather than being most available in the currents at the edge of the reef, are widespread over the reef, so aggregation in response to a clumped food resource doesn't occur. The threat from visual predators is apparently much reduced at night, so aggregation as a defensive response to predators also doesn't occur (Hobson 1991). Morphologically, nocturnal planktivores lack the streamlined bodies and forked tails characteristics of fast swimming fishes, which suggests that maintaining station in a strong current (or rapid swimming to escape a predator) is not a problem regularly encountered by these fishes.

For a thorough review of planktivory by fishes inhabiting coral reef ecosystems, see Hobson (1991).

**Carnivores**

Carnivorous fishes exhibit an amazing array feeding morphologies, from the tiny, specialized mouths of fishes like forceps butterflyfishes (*Forcipiger* spp.) to the large, generalized mouth structure common in so many species of scorpionfish (*Scorpaenidae*), snapper (*Lutjanidae*) and sea bass (*Serranidae*). As might be expected from the diverse feeding morphologies, the range of prey items taken includes both invertebrates (sessile and mobile, from hard and soft bottom habitats) as well as
fishes. Vertebrates other than fishes may also be taken by some species. Juvenile turtles may be consumed by reef fishes shortly after hatching, while adult turtles are taken by large sharks, especially the tiger shark (*Galeocerdo cuvier*). In addition, birds (especially newly fledged individuals) may be taken by sharks like the tiger shark.

Carnivorous species of reef fishes are more common on coral reefs than their herbivorous or planktivorous counterparts. Jones *et al.* (1991), in their review of fish predation and its impact, evaluated data from seven studies on the diets of coral reef fishes (Hiatt and Strasburg 1960, Randall 1967, Goldman and Talbot 1976, Hobson 1974, Williams and Hatcher 1983, Sano *et al.* 1984, and Thresher and Colin 1986), and calculated the proportion of fish species in different trophic categories. Carnivorous species (piscivores and benthic invertebrate feeders, not including planktivorous species) were the most common in all seven investigations, ranging from a high of 68% of the species present to a low of 41%. Herbivores ranged from about 25% to 7% of species present, planktivores ranged from 38% to 4%, and omnivores ranged from 19% to 4%.

Among carnivores, fishes specialized to consume benthic reef invertebrates appear to be more prevalent than piscivores. In five of the seven feeding studies cited by Jones *et al.* (1991), benthic invertebrate predators were the most speciose trophic group, accounting for between 56% and 27% of the species present. Piscivores comprised between 37% and 4% of the species present in those studies. Invertebrate predators and piscivores are discussed below, beginning with fishes that feed on invertebrates.

Major categories of fishes that feed on benthonic invertebrates include coral-polyp feeders, sessile invertebrate feeders, feeders on mobile invertebrates, and omnivores which are frequently primarily carnivorous (Jones *et al.* 1991). Fishes which feed on mobile invertebrates are far more numerous than those consuming coral polyps or other sessile invertebrates [45-34% of the species in the seven studies cited by Jones *et al.* (1991) versus 9%-1% and 13%-3% for the other two categories respectively].

Among mobile invertebrates, crustaceans may be particularly important prey on coral reefs. For example, in their study of fishes from the Northwestern Hawaiian Islands, Parrish *et al.* (1985) found that benthic crustaceans comprised 75% of the dietary items consumed by percent occurrence in stomachs (53% by numbers, 48% by weight), and consisted mainly of crabs (about half), followed by shrimps, amphipods, and stomatopods. Molluscs were a distant second to crustaceans as dietary items (21.5% by occurrence, 21.3% by numbers, and 11.1% by weight), with other benthonic invertebrate taxa like polychaetes and echinoderms rarely showing up in stomach contents (<5% by any measure). Fishes foraging over soft sediments for mobile invertebrate prey appear to consume mainly molluscs (G. P. Jones, D. J. Ferrell, and P. 23
Benthonic invertebrate predators may exhibit selectivity in prey items consumed (i.e. the relative abundance of prey items in their diets does not simply mirror prey abundances in the environment), although relatively few investigators have quantitatively estimated prey abundances for comparison with dietary arrays (Jones et al. 1991). Parrish et al. (1985) sampled the benthic biota of patch reef habitats in the Northwestern Hawaiian Islands for comparison with their fish dietary data. Their results suggest that crustaceans and molluscs are targeted by invertebrate feeding fishes (Jones et al. 1991). Crustaceans were almost twice as abundant by weight in fish stomachs compared to their field abundance, while molluscs were almost four times more abundant by weight in fish stomachs than in the field. Conversely, echinoderms, worms, and sponges were much more abundant in the field than in the stomachs of fishes, suggesting avoidance of these taxa. Guzman and Robertson (1989) compared coral availability to coral consumption by the corallivorous pufferfish Arothron meleagris in the eastern Pacific. Their results indicated that coral consumption by this fish was not simply a reflection of coral species abundance. Feeding preference for various coral species varied between study locations. At some locations, common corals (Pocillopora and Porites) made up the bulk of the diet while at others, rare corals (Psammocora) made up the bulk of the diet. Furthermore, the relative proportion of corals consumed was subject to change with time and not related in a consistent way to changes in abundance.

Foraging by sessile invertebrate feeding fishes can have a pronounced impact on the distribution and abundance of their prey (Jones et al. 1991). Sponge distributions may be influenced by the action of grazing carnivores, with sponge populations being confined to areas where grazing pressure is less intense (Bakus 1964 as cited by Jones et al. 1991). Grazing carnivores can also effect overall species diversity in sessile invertebrate communities (Jones et al. 1991). In a series of experimental manipulations inside caves at Heron Island, Day (1977, 1985) was able to demonstrate that areas grazed by fishes had invertebrate species diversity approximately 20% higher than in experimental plots where grazing was prevented by cages. Fishes (primarily pomacanths and balistids), in preferentially selecting ascidians (tunicates), increased survival of competitively inferior encrusting fauna like bryozoans.

Coral feeding fishes can effect corals in a direct negative way (i.e. by consuming them), or in indirect ways either positive or negative (i.e. by altering the outcome of competition between coral species through their foraging activities) (Glynn 1988, 1990). Corallivorous fishes can exhibit profound direct effects on the distribution of their coral prey. For example, in Guam the coral Pocillopora damicornis suffers a pronounced reduction in its potential depth distribution as a result of predation from corallivorous fishes (Neudecker 1977). While able to survive in water 30 m deep, and grow rapidly at 15 m of depth, the coral is essentially restricted to the reef flat, crest, and lagoons.
because of intense predation pressure by corallivorous fishes in deeper water.

Selective predation by fishes on competitively dominant corals (direct effect) can provide a competitive release for subordinate coral species (indirect effect) (Glynn 1988, 1990, Lang and Chornesky 1990). Cox (1986) investigated the effect of predation by the corallivorous butterfly fish, Chaetodon unimaculatus, on competition between Montipora verrucosa and Porites compressa in Kaneohe Bay, Hawaii. She found that C. unimaculatus, which preferentially feeds on the competitively dominant M. verrucosa, reduces competitive stress on the subordinate P. compressa. In the presence of the corallivore, P. compressa enjoyed increased abundance and distribution.

Fishes feeding on mobile invertebrates can also influence the distribution and abundance of prey species (Jones et al. 1991). For example, in coral reefs off of Kenya it appears that the abundance and distribution of urchins, primarily boring urchins (Echinometra mathaei), is markedly affected by predation from fishes (McClanahan and Muthiga 1989, McClanahan and Shafir 1990). On four reefs historically subject to heavy fishing, fish densities were low and urchin densities were high. On two reefs where fishes were protected, fish densities were about 4x higher and urchin densities about 100x lower. McClanahan and Muthiga (1989) attributed 90% of urchin mortality in Kenya to predatory fishes. McClanahan and Shafir (1990) identified the balistids Balistaphus undulatus and Rhinecanthus aculeatus as the dominant fish predators involved. On natural (unfished) reefs, boring urchins were found primarily on the reef flat with numbers declining sharply with depth (McClanahan and Muthiga 1989). The decline was attributed to increased predation pressure by fishes in deeper regions of the reef. On fished reefs where piscine predation on the urchins was reduced, E. mathaei expanded its distribution into deeper water.

The effects of predation by fishes on invertebrates may not only relate to consumption of their prey, but also to disturbance of the habitat by the foraging fishes which may effect neighboring invertebrates (Jones et al. 1991). Unfortunately, separating these two sources of impact is often very difficult (Jones et al. 1988).

It appears that predation by fishes may influence the distribution, abundance, and species diversity of benthonic invertebrates on coral reefs as well as operating as a major selective force leading to the evolution of defensive mechanisms by invertebrate prey (Bakus 1966, 1969, 1981, 1983 as cited by Jones et al. 1991). Additionally, it has been hypothesized that the influence of fish predation on invertebrate communities increases from temperate to tropical systems (Bakus and Green 1974; Green 1977; Vermeij and Veil 1978; Bakus 1964, 1981, 1983; Bertness 1981 as cited by Jones et al. 1991). Unfortunately, much of the work done to date in the area of fish predation on invertebrates is from temperate systems or focuses on trophic groups other than those consuming benthonic invertebrates (Jones et al. 1991). More work needs to be done before the impact of piscine predators on coral reef invertebrates is fully understood.
Piscivorous fishes, although not as prevalent as invertebrate feeders, are still relatively common on coral reefs. Hixon (1991), citing data from nine regional surveys of coral reef fish diets (Hiatt and Strasburg 1960, Talbot 1965, Randall 1967, Hobson 1974, Goldman and Talbot 1976, Brock et al. 1979, Harmelin-Vivien 1981, Williams and Hatcher 1983, and Parrish et al. 1986) reports that 8% to 53% of the fish species on coral reefs consume other fishes, at least as part of their normal diet. Hixon (1991) goes on to point out that piscivorous fishes are sometimes very abundant in addition to being diverse, citing work by Goldman and Talbot (1976) which reported that piscivores accounted for 54% of the total fish biomass at One Tree Island on the Great Barrier Reef. Clearly, fishes which consume other fishes, are an important trophic group on coral reefs.

Morphologically, piscivores have for the most part remained fairly close to the generalized, large-mouthed carnivorous ancestors hypothesized for teleost fishes by Schaeffer and Rosen (1961) and Gosline (1971), although some groups exhibit structural specializations related to feeding like tubular mouths (i.e. trumpetfishes) or highly modified body morphology (i.e. frogfishes). Most piscivores have large mouths, with jaws exhibiting various degrees of protrusibility. Many, though not all, have distendable buccal cavities, which enlarge when they strike creating a sucking action which may facilitate the capture of prey. Most possess conical, inward-slanting teeth for piercing and holding piscine prey prior to swallowing them whole (Lagler et al. 1977). The gill-rakers of piscivores (and many other carnivores) are short, stout, and widely spaced (Moyle and Cech 1988). The pharynx of piscivores is usually large and distendable, and their stomachs tend to be elongate and tubular in shape (Lagler et al. 1977). The gut is short indicative of the digestibility of piscine prey (Lagler et al. 1977, Moyle and Cech 1988).

Behaviorally, piscivores exhibit diverse foraging strategies. Hixon (1991) referring to the work of Hobson (1975, 1979) outlined five major piscivore feeding categories: 1) open-water species like jacks which pursue their prey (Potts 1981); 2) cryptic species like lizardfishes and scorpionfishes which ambush their prey (Sweatman 1984); 3) species like groupers and snappers which seem to habituate prey to the illusion that they are nonpredatory (Harmelin-Vivien and Bouchon 1976); 4) species like trumpetfishes which slowly stalk their prey (Kaufman 1976); and 5) species like moray eels that locate prey within crevices (Bardach et al. 1959). These various hunting strategies are not necessarily mutually exclusive and the final attack by all piscivores involves a sudden and extremely rapid strike (Hixon 1991).

Additionally, some species utilize aggressive mimicry to capture prey (Hixon 1991). Aggressive mimics lull prey into complacency by resembling nonpiscivorous species or lure prey by resembling, in some way, prey items. Trumpetfish have been
reported to exhibit the former type of aggressive mimicry by hiding among herbivorous fishes (Aronson 1983). As an example of the latter variety of aggressive mimicry, the scorpionfish *Iracundus signifer* lures other piscivores to their deaths by slowly moving their dorsal fin which resembles a small fish (Shallenberger and Madden 1973). Perhaps the most amazing of the piscivorous aggressive mimics are the frogfishes which capture prey fishes by waving a lure-like dorsal fin spine in front of their mouths (Pietsch and Grobecker 1978).

Prey fishes have evolved numerous anti-predatory adaptations. Hixon (1991), in his review of fish predation and its impact on the community structure of coral reef fishes, summarized the adaptive responses of prey fishes to predation pressure from reef piscivores. The basic categories of defensive response outlined and discussed by Hixon were morphological, chemical, and behavioral.

Morphological adaptations include both structural features and coloration. As previously mentioned, many reef fishes are very deep bodied (damselfishes, angelfishes, butterflyfishes, trigger/filefishes, etc.). Combined with spinous fin rays, these fishes are presumably difficult to swallow, especially if taken from behind which causes the rear-ward projecting spines to catch in the throat and further erect. Some fishes are able to dramatically increase body size by inflation (puffers, porcupinefishes), thereby making it very difficult for predators to swallow them. Finally, some prey fishes utilize a streamlined body and rapid swimming to elude fast swimming piscivores (Hobson and Chess 1978). Young parrotfishes may deter nocturnal predation by moray eels by secreting a mucus "cocoon" which presumably prevents the olfactory-oriented morays from detecting their scent while they lay inactive on the bottom (Winn and Bardach 1959).

Coloration can be used in a variety of ways to deter predators. Cryptic coloration (camouflage) is widespread among benthic reef fishes (gobies, blennies, scorpionfishes, flatfishes, etc.) allowing them to match the background or to resemble inedible objects like stones or sea grasses (Randall and Randall 1960, Hixon 1991). Many reef fishes have alternating bright and dark colored bars on their bodies (i.e. juvenile angelfishes, scorpidids, some damselfishes) which are thought to camouflage the individual by disrupting its outline when viewed against features of the bottom or other similarly colored individuals (Lagler et al. 1977). False eye spots on the tail combined with coloration masking the eye (i.e. some butterflyfishes and anglefishes) may cause predators to misdirect attacks (Lagler et al. 1977, Neudecker 1989). Some prey species utilize Batesian mimicry (i.e. a harmless or palatable species mimicking a harmful or unpalatable species) to avoid predators. For example, the plesiopid *Calloplesiops altevelis*, when startled exhibits behavior and coloration which mimics the spotted moray eel, *Gymnothorax meleagris* (McCosker 1977). In another example of Batesian mimicry, the cardinalfish *Fowleria* sp. (harmless mimic) resembles the scorpionfish *Scorpaenodes guamensis* (venomous model) (Seigel and Adamson 1983).
Finally, some fishes exhibit aposematic coloration (warning coloration) advertising the fact that they are venomous (pectoral flashing by some scorpionfishes, directive markings near the caudal "blades" of some surgeonfishes), toxic (some puffers), or unpalatable (some butterflyfishes) (Neudecker 1989, Hixon 1991).

Venoms and toxins, often combined with aposematic coloration, may deter piscivores. For example, all scorpionfishes (Scorpaenidae) possess venomous fin spines. Most tropical species are cryptically colored, and many are ambush predators on other fishes. However, if alarmed, many of these cryptic fishes suddenly erect their fin spines and expose brightly colored pectoral fin axillary surfaces with rapid "flashing" movements (personal observation). This startling display, combined with the fact that they are venomous, probably deters predators. Venomous weeverfishes (Trachinidae) are reported to exhibit warning displays when alarmed (Bond 1979), and the blennid Meiacanthus atrodorsalis has a venomous bite (Losey 1972). Furthermore, many fishes have toxic tissues or excretions which are thought to deter predators. The most notorious of those are the Tetraodontiformes (pufferfishes and their allies) which have the potent neurotoxin, tetrodotoxin, in their tissues (Halstead 1978, Gladstone 1987, Hixon 1991). Other fishes reported to possess toxins in their skin include some moray eels, soapfishes, some gobies, and some flatfishes (Hixon 1991).

Prey fishes have evolved a host of different anti-predatory behavioral adaptations in response to piscivores. Beyond the obvious adaptations of staying near shelter and flight at the moment of attack, fishes exhibit more subtle anti-predatory behaviors including schooling, and temporal adjustment of spawning and daily activity patterns to minimize the effect of predators (Hixon 1991). While schooling may afford fishes adaptive advantages other than just anti-predatory benefits (i.e. improved foraging success, hydro-dynamic drag reduction), there is widespread agreement that avoiding predation is a major reason why so many reef fishes school or aggregate (Hixon 1991). Among the anti-predatory advantages of schooling are: 1) aggregated prey have a reduced probability of encountering random search predators compared to dispersed prey; 2) for each individual there is a reduced mathematical probability of being consumed when a predator does attack; 3) predator "misses" increase relative to strikes on isolated prey presumably because predators have a difficult time visually "locking onto" any one individual among the moving mass of prey; and 4) most individuals in the school begin to take evasive action before ever seeing the attacking predator because all fishes in the school respond almost instantly to the evasive actions of individuals on the edge of the school who have seen the approaching predator (Hamilton 1971, Shaw 1978, Partridge 1982, Pitcher 1986, Hixon 1991).

Beyond schooling, reef fishes reduce the effect of predation by adjusting important activities in response to the threat from predators. Hixon (1991) citing the work of Johannes (1978, 1981) points out that most reproductive behaviors exhibited by tropical reef fishes appear to be designed to reduce predation on themselves or their
eggs/larvae. For broadcast spawners (most marine fishes), offshore spawning migrations reduce predation on eggs/larvae, spawning near shelters reduces predation on the spawners, vertical spawning rushes reduce the time spawners are exposed and reduces predation on eggs by releasing them away from the bottom, spawning during ebbing spring tides reduces predation on eggs/larvae because tidal action moves them offshore, and spawning at night reduces predation on both spawners and eggs. Demersal spawners defend their broods which reduces predation on eggs, and live-bearers eliminate predation on eggs/larvae.

Finally, tropical reef fishes adjust their basic daily activity patterns to minimize the effect of visual piscivores (Hobson 1972, Collette and Talbot 1972, Domm and Domm 1973). Basically, during the twilight periods of dawn and dusk, fishes susceptible to predation by visual predators are inactive in shelters on the reef. These twilight periods of inactivity, each lasting about 15 minutes, were coined the "Quiet Period" by Hobson (1972). On the Kona Coast of Hawaii, the evening quiet period occurs approximately 15-30 minutes after sunset, while the dawn quiet period lasts from about 45-30 minutes before sunrise (Hobson 1972). During these crepuscular periods, the visual systems of both diurnal and nocturnal prey fishes are ineffective for detecting piscivores (McFarland 1991). Conversely, the visual systems of piscivores achieve maximum sensitivity at twilight (Hixon 1991). The threat of predation during crepuscular hours has resulted in rigid structuring of the activity patterns of both diurnal and nocturnal prey fishes, mandating relative inactivity during the period of greatest piscivore advantage (Hobson 1972).


Patterns of Spacing in Coral Reef Fishes

How coral reef fishes are distributed spatially in their environment is an important aspect of their social structure and can provide clues to their natural history. Spacing patterns in coral reef fishes are diverse, ranging between solitary species which do not regularly interact socially with conspecifics to species which form social groupings like aggregations of territorial individuals or aggregations/schools of nonterritorial individuals. As important as spacing is, it is only one aspect of the social organization or structure of coral reef fishes. A thorough treatment of this complex subject is beyond the scope of this chapter. For a more extensive discussion of social organization in coral reef fishes, see Sale (1980a, pp. 379-387), Shapiro (1991) or Warner (1991).

Coral reef fishes that spend the majority of their time as truly solitary individuals
appear to be uncommon (personal observation). Many territorial fishes, which on first 
impression appear to be solitary, are in fact clustered with other territorial individuals of 
the same species and cannot therefore be considered "solitary" (see discussion below). 
Perhaps the most common solitary fishes on Hawaiian coral reefs are roaming or site-
attached piscivores like some jacks, trumpetfish, barracuda, sharks, etc. (personal 
observer). In Hawaii, even these "solitary" species are often seen in twos or threes 
(i.e. jacks). In other areas of the world these kinds of fishes (i.e. jacks, sharks, 
barracuda) may occur in large aggregations or schools, depending upon species. In 
summary, truly solitary fishes (i.e. individuals that do not regularly interact socially with 
conspecifics) are relatively uncommon on coral reefs.

A number of coral reef fishes occupy and defend territories. Territoriality is a 
form of interference competition in which a defined space is defended on a temporary or 
permanent basis for the purpose of securing a limiting resource. For coral reef 
fishes, territorial boundaries contain food, shelter, spawning site, or a combination of 
these factors (Shapiro 1991). Territoriality in coral reef fishes has been particularly well 
studied in the damselfishes, but many other families like the butterflyfishes and 
surgeonfishes have also received attention. Only a couple of representative examples 
of fish territoriality will be mentioned here.

Low (1971), working on the Great Barrier Reef, conducted one of the first 
comprehensive investigations of territoriality in a coral reef fish. He studied territorial 
behavior in the damselfish, *Pomacentrus flavicauda*, a herbivorous species which 
forages on filamentous algae growing on dead coral within its territorial boundaries. 
This damselfish exhibited interspecific territorial defense, responding agonistically 
toward 38 different species from 12 different families, while ignoring 16 other species 
from 6 families. Thirty-five of the 38 species that were attacked were herbivores or 
omnivores. The 16 species that were ignored were carnivores. The 3 carnivore 
species attacked were large wrasses of the genus *Choerodon* which forage by 
overturning coral boulders. These boulders are used by the damselfish for shelter and 
for protection of eggs which are also laid on the territory. Low concluded that 
territoriality in *P. flavicauda* was primarily a function of defense of food resources.

Tricas (1985), working in the reefs off Puako, Hawaii, studied space utilization in 
the territorial brown-barred butterflyfish, *Chaetodon multicinctus*. Adults are 
monogamous, obligate coral feeders (Reese 1975). Tricas discovered that this species 
defends feeding territories against intrusion by conspecifics, other corallivorous 
butterflyfishes like *C. ornatusimus* and *C. quadrimaculatus*, and even a corallivorous 
damselfish (*Plectroglyphidodon johnstonianus*). Feeding territories at Puako averaged 
about 57 m$^2$ in area, were defended by a male/female pair, and shared contiguous 
borders with other *C. multicinctus* territories that changed only slightly over the course 
of a year. Pair fidelity was strong over the short term, and though usually not lasting 
more than a year, at least one pair remained together in the same territory for more than
three years. The primary food resource defended by *C. multicinctus* at Puako was lobe coral, *Porites lobata*, which comprised about 70% of the fish's diet.

 Territory boundaries are not always static in time and may change seasonally or in response to different intruders. Myrberg and Thresher (1974) studied territorial behavior in males of the herbivorous threespot damselfish, *Eupomacentrus planifrons*, in the Florida Keys. They found that the level of aggressive response varied with the species of intruder, with some species being attacked farther from the territory center than others. Conspecifics were always attacked farthest from the territory core, followed by congeners (members of the same genus), and finally noncongeners. In addition, Myrberg and Thresher found a seasonal shift in attack radius (i.e. aggressive intensity) for most species of intruder. For most species, attack radius increased from a minimum in January to a maximum in April. This change corresponds to aspects of the annual reproductive cycle in this species. Eggs are deposited in male territories and are then defended by the resident male. Reproductive activity peaks in April and is at a minimum in January, and agonistic behavior associated with egg defense reflects this change in reproductive activity. The authors conclude that *E. planifrons* defends "serial" territories which contain more than one limiting resource, in this case both food and reproductive site, and whose area of defense varies depending upon species of intruder and time of year.

 Territory size may also change in response to changes in resource or population density. How territory size changes in response to changes in these variables (i.e. whether it expands or contracts) depends upon a number of life-history traits of the species in question. This is a surprisingly complex theoretical subject, and to elaborate upon it here would be inappropriate. For additional information on optimization of territory size consult Brown (1964), Ebersole (1980), Harvey and Mace (1983), Hixon (1980, 1987), Schoener (1983), Shapiro (1991), and Warner (1991).

 There is a growing body of evidence to suggest that territorial coral reef fishes cluster in aggregations, although few studies have been done in which territories have been mapped over a large enough area to document clumping statistically (Shapiro 1991). However, Sadovy (1986 as cited by Shapiro 1991) mapped territories of the Caribbean damselfish, *Stegastes partitus*, and was able to statistically document that this species occupied territories that were aggregated in clusters. Sadovy also discovered that members of some clusters did not interact behaviorally with members of others, and referred to these discrete aggregations as "colonies".

 Clustering of territories into "colonies" may confer a number of advantages to colony members which were reviewed by Shapiro (1991). Members may gain increased protection from predators since clustering reduces each individual's probability of being consumed when a predator strikes. They may also gain increased protection from interspecific food competitors because entry into each member's
territory is blocked in part the territories of other members of the colony. Distance and time needed to find a mate is lessened by clustering, reducing the time that members spend off their territory. This in turn reduces the time they are away from shelter and exposed to predators. It also reduces the time in which food resources on the territory are unprotected. Reduced food loss to competitors may allow individuals in colonies to hold smaller, easier to defend, territories than they would if they were more isolated. In addition, neighbors may form alliances to help defend each other's territory against incursions from potential territorial usurpers.

Many nonterritorial species of coral reef fishes will form aggregations or schools. The proximal stimulus for aggregation/schooling is usually social attraction, although ultimately these grouping form in response to a localized resource like mates or food, or in response to attacks by visual predators. Before proceeding, differences in the structural and behavioral characteristics of aggregated and schooled fishes should be briefly mentioned. An aggregation of fishes may consist of several different species. Furthermore, individuals in the aggregation are often of different sizes and generally are not all oriented in the same direction. Fishes in a school are usually all of the same species, are similar in size, are generally oriented in the same direction, and swimming in unison. Sometimes the term "unpolarized school" is applied to aggregating fishes, while fishes meeting the criteria listed above for schooled fishes are said to be in a "polarized school". The majority of coral reef fishes which group socially form aggregations rather than schools.

Examples of aggregating nonterritorial coral reef fishes are too numerous to list. Many fishes on the reef aggregate around food resources. As mentioned in the previous section on trophic interactions, many herbivorous fishes aggregate in areas of the reef where plant resources are most abundant. Likewise, diurnal planktivores form aggregations at the reef's edge where currents bringing zooplankton to the reef are strongest. These aggregations, which sometimes become schools, also confer some additional advantages beyond access to needed resources. As mentioned earlier in the trophic ecology section, schools and aggregations are effective anti-predatory adaptations which reduce each individual's probability of being consumed by a piscivore. In the case of herbivores like surgeonfishes, schooling/aggregating is also an effective foraging strategy in regard to swamping the defense system of territorial herbivores like damselfishes (Robertson et al. 1976). For example, when a solitary manini (*Acanthurus sandwicensis*) enters the territory of a Pacific Gregory (*Stegastes fasciolatus*), it will be immediately chased out and rarely manages to feed prior to eviction. However, when a school of manini enter that same damselfish's territory, some individuals manage to feed while the damselfish is busy chasing others out of its territory.

Not all aggregations of coral reef fishes center around food resources. In the bluehead wrasse (*Thalassoma bifasciatum*), a species where protogynous
Hermaphroditism is common, females may aggregate around solitary males for the purpose of breeding. Before discussing aggregating behavior of the bluehead wrasse, a brief review of sequential hermaphroditism is appropriate. A sequential hermaphrodite is a fish which starts out life as one sex and later changes morphologically and behaviorally to become the opposite sex (in spite of these changes their genetic sex does not change). Fishes which start out life as females and change sex to become males are called protogynous hermaphrodites. This is probably the most common type of sequential hermaphroditism in fishes and is frequently seen in the labrids, scarids, and serranids. Fishes which start out life as males and change sex to become females are called protandrous hermaphrodites. This is apparently a rarer phenomenon in the fishes but has been reported in a number of families including the Gonostomatidae or bristlemouths, Serranidae or sea basses, Sparidae or porgies, Centracanthidae - no common name, Labridae or wrasses, and Playtecephalidae or flatheads (Bond 1979). For a theoretical analysis of hermaphroditism among animals see Ghiselin (1969). For more information on sequential hermaphroditism in fishes consult the numerous publications of Robert R. Warner (for a sampling see Warner et al. 1975; Warner 1975, 1988a.b, 1991) and Douglas Y. Shapiro (for a sampling see Shapiro 1979, 1980, 1984, 1987, 1989, 1991).

Returning to the bluehead wrasse, large males set up and defend mating territories on elevated portions of the downcurrent edge of the reef (Warner 1991). These territories serve as "egg-launching" sites for the species' pelagic eggs. Females spend most of their time feeding upcurrent of the male breeding sites, but when they are ready to mate, they migrate to a mating site, spawn, and then return to the feeding area (Warner 1991). Females frequently arrive in sufficiently large numbers that groups of them await their turn to spawn with a male. In addition, some mating sites are not defended by a solitary male, but are instead occupied but not defended by groups of smaller males. These aggregations of small males mate in groups with arriving females (Warner et al. 1975). Basically, in the bluehead wrasse, either females or males may form nonterritorial aggregations around reproductive resources (i.e. the opposite sex).

Before concluding, it is important to realize that for most species, social organization or spacing patterns will change ontogenetically (Helfman 1978, Shapiro 1991). The mode of spacing utilized will therefor change depending upon the life history stage of the species in question or even upon time of day (i.e. postlarvae, early stage juvenile, late stage juvenile, adult). Shapiro (1991), in a review of intraspecific variability in coral reef fish social systems, provides a number of examples of this ontogenetic variation in social organization. One example concerned the French grunt, Haemulon flavolineatum, in the Caribbean. Immediately after recruiting from the plankton, the smallest postlarvae form mixed schools with mysid shrimps hovering near the bottom over sea urchins or corals. Slightly larger juveniles form size-specific schools associated with particular coral heads. Size uniformity in school members is thought to increase locomotor efficiency and reduce the risk of predation. Large juveniles are
territorial, defending small territories over crevices or coral heads. Territories are also thought to provide protection from predators. At night, all individuals migrate off the reef to feed at nearby sea grass beds.

Another example of ontogenetic sequencing of social structure reviewed by Shapiro concerns the protogynous redband parrotfish, *Sparisoma aurofrenatum*, of the Caribbean (Clavijo 1982 as cited by Shapiro 1991). Individuals mature as females which reside in territories of males where most reproduction occurs. Later in life females leave the territories, wander briefly as females, change sex, and then wander as males. Eventually these wandering males occupy a territory, and then spawn with females in that territory. Individuals apparently shift from occupying territories to wandering at the onset of sex change because newly sex-changed males improve their reproductive output by locating vacant territories already containing two to five females rather than remaining in their original territory to compete for females with the resident male who is much larger. In summary, social structure in the redband parrotfish is ontogenetically determined and is reflected in three patterns of space use: occupying territories as juveniles and young adult females, wandering as females and then as males, and finally re-occupying territories as males.

**Community Structure of Coral Reef Fishes**

Coral reef communities harbor extremely diverse fish assemblages which, near the Indo-west Pacific center of tropical diversity, may number in the thousands of species (Briggs 1974, Ebeling and Hixon 1991). How this high diversity is maintained has been the source of considerable, and long-standing, debate (Hixon 1991). At the most fundamental level, there are two basic views on how assemblages of competing species on coral reefs might be organized. Those perspectives have been referred to as the "equilibrium" and "nonequilibrium" views of community structure (see Connell 1978).

In the equilibrium view, species composition is a consequence of past and present interspecific competition (i.e. competition between different species). Interspecific competition is thought to result in a situation in which each species occupies space or consumes food resources for which it is the most effective competitor (Connell 1978). If there is no environmental perturbation, species composition of the community persists through time; if perturbation occurs, community composition is restored, through competition, to its original state (Connell 1978). In the nonequilibrium view, natural disturbance and environmental change disrupt communities, often in an abrupt and unpredictable manner (Connell 1978). Proponents of this view postulate that the frequency of natural perturbation is sufficiently high that communities rarely fully recover (reach "equilibrium") before more disturbance occurs. Because "equilibrium" is rarely attained, competitively subordinate species are not inexorably excluded from the
On the coral reef, myriads of fish species with very similar resource requirements seem to coexist in stark contrast to predictions based on equilibrium theory. This has troubled fish biologists and community ecologists for almost two decades and has lead to the formulation of a number of opposing hypotheses postulated to explain the high diversity of tropical reef fishes. Generally, the hypotheses concerning coral reef fish community structure fit into one of four basic models (Jones 1991): 1) the Competition model, 2) the Lottery model, 3) the Predation-Disturbance model, and 4) the Recruitment-Limitation model (for an alternate, though related, listing and discussion of hypotheses concerning the community structure of coral and temperate reef fishes, see Ebeling and Hixon 1991, pp 537-560). The Competition model falls within the equilibrium view of community structure, while the remaining three models are all variants of the nonequilibrium view. Each model is discussed in more detail below.

**Competition Model**

The Competition model, essentially synonymous with the equilibrium view of community structure, assumes that the number and type of fish species found on coral reefs is determined through competition for limited resources (Smith and Tyler 1972, Smith 1978). As pointed out by Ebeling and Hixon (1991), in their review of tropical and temperate fish communities, this "niche diversification" model has two versions. The first proposes that as a result of competition for limited resources over evolutionary time, coral reef fishes have become resource specialists and competitive exclusion is prevented. The second assumes that competition is currently occurring among fishes occupying coral reefs. Competitive exclusion doesn't occur because the environment either provides resource refuges for subordinate competitors (i.e. a suboptimal area or food items not preferred by the dominant competitor and hence available to the subordinate) or because each competitor is dominant in a particular subhabitat or in regard to utilizing some subsection of a resource base like food. In either case, coral reef fishes should exhibit some form of "resource partitioning" like eating different arrays of prey, residing and/or foraging on different parts of the reef, or being active at different times of day (Ebeling and Hixon 1991).

The competition or niche diversification model postulates that the high species diversity exhibited by fishes in coral reef ecosystems is attributable to an abundance of species which utilize narrow and finely partitioned niches (i.e. that it is because of fine-grained resource partitioning which is ultimately attributable to competition) (Mead 1970, Briggs 1974, Ebeling and Hixon 1991). There is considerable evidence to suggest that resource partitioning does occur widely among fishes inhabiting coral reef environments. Of 38 investigations cited by Ebeling and Hixon (1991) which investigated possible resource partitioning by tropical marine fishes, 82% found evidence of resource partitioning (see pp. 539-542 of Ebeling and Hixon for a tabular...
The common occurrence of resource partitioning among coral reef fishes suggests that the competition or niche diversification model has merit. However, caution may be advised. Citing Ross (1986), Ebeling and Hixon warned that resource partitioning may simply reflect chance divergences in the evolutionary histories of the species involved and may have nothing to do with competition. Peter Sale remarked: "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?" (personal communication cited by Ebeling and Hixon 1991). That coral reef fishes partition resources on the reef is irrefutable. Whether that partitioning is always indicative of underlying competition for limited resources remains a source of contention among coral reef ecologists.

**Lottery Model**

The Lottery model, the first to deviate from traditional ecological thought, maintains that chance recruitment of fishes to the reef and their subsequent ability to competitively hold onto limited space determines species composition on the reef (Sale 1974, 1977, 1978, 1991c; Sale and Dybdahl 1975). Sale (1974), in studying ecologically similar and co-occurring territorial damselfishes on the Great Barrier Reef, concluded that although there was some evidence of partitioning of food and habitat among the damselfishes, resource utilization by the fishes exhibited great overlap. Furthermore, removal of individuals produced major changes in territorial boundaries and species composition which persisted through time. Sale concluded that coexistence among the damselfishes, "appears to be maintained primarily because recruitment of juveniles is an essentially chance process depending upon (a) the random creation of vacant living space, and (b) the uncontrolled dispersal of the pelagic larvae."

Sale and Dybdahl (1975), in another investigation on the Great Barrier Reef, did successive collections of all fishes occupying replicate heads of living and dead coral (dubbed "L-units" and "D-units" by the authors) approximately every four months over a period of about two years. They discovered that the living and dead coral units were remarkably similar in regard to the composition of fishes collected from them (i.e. relatively few species exhibited a strong preference for L or D units). They also discovered that for any specific coral head, the assemblages of fish species captured on successive collections could be quite different from collection to collection.

Sale and Dybdahl's results didn't fit the equilibrium view of community structure which would have predicted very different species assemblages for live and dead units.
(i.e. resource partitioning of very different habitat types), and would have predicted that specific units would be repeatedly occupied by similar assemblages of species (i.e. predictable recruitment of species based on resource needs matching those available in the vacated coral heads). While acknowledging that on a large scale fishes may partition their habitat spatially, they concluded that on a small scale the distribution of species reoccupying vacated coral heads was the result of chance colonization, not of a systematic partitioning of living space. Once a coral head is fully filled with colonists, those fish successfully hold onto that space until they die or are removed by some form of disturbance.

Since those early pioneering reports, Sale has written many articles which elaborate upon and refine the Lottery model (Sale 1977, 1978, 1979, 1980a&b, 1985, 1991c). Nonetheless the core of the original hypothesis remains intact; coral reef fish community structure is determined largely by chance recruitment of larval fishes onto patches of newly-vacated and limiting space on the reef. These communities are "open nonequilibrial systems" in which reef fish species exist in spatially divided populations in a patchy environment (Sale 1991c, Mapstone and Fowler 1988). Local populations export all gametes/larvae to the open ocean and receive new recruits from the open ocean, almost certainly recruits produced by other populations (Sale 1991c). Local recruitment of each species is therefore independent of local reproductive success, relying instead on success of other populations. Sale (1991c) points out that the decoupling of reproduction and subsequent recruitment "means that even strong interspecific competition among local residents cannot lead to permanent local extinction, nor to a coevolved partitioning of resources in the manner predicted by classical competition theory." High larval mortality during the planktonic phase can add to the unpredictability of larval recruitment onto the reef and may ultimately lead to change in community structure (Sale 1991c, Jones 1991).

In conclusion, reef fish compete with each other through their planktonic larvae to obtain limiting resources which are both patchy in distribution and unpredictably available. Diversity of fishes on the reef is high because species with highly overlapping resource requirements coexist, not through resource partitioning, but rather by recruiting to and holding small patches of space on the reef. In this regard, the reef might be viewed as a patch-work quilt of stochastically recruited species assemblages.

**Predation Disturbance Model**

The Predation-Disturbance model assumes that adult populations are held below the level at which resources become limiting through postsettlement mortality of juveniles and adults from predation and that competitive exclusion therefore does not occur (Goldman and Talbot 1976; Johannes 1978; Talbot et al. 1978; Bohnsack and Talbot 1980; Hixon and Beets 1989, 1993; Hixon 1991). This hypothesis has not received as much attention as some of the others which, according to Hixon (1991), is
surprising given the attention predation has received in behavioral and community ecology and in marine fisheries biology.

Hixon (1991), in a review and analysis of predation's role in structuring coral reef fish communities, points out that the predation hypothesis has generated two basic predictions. First, if predation is important, prey fishes should be morphologically and behaviorally adapted to minimize the risk of predation. Second, the abundance of prey species should shift predictably when the density of predators or prey refuges changes.

The first prediction appears to be substantiated by the diverse anti-predatory adaptations that have evolved among prey fishes, as well by the ubiquity of piscivores on the reef and their own adaptations for successfully securing prey. The wide array of predator and prey adaptations (morphological, chemical, and behavioral) among reef fishes were discussed previously in the "Carnivores" subsection of the Trophic Ecology section of this chapter. Although evolutionary evidence is indirect or circumstantial it nonetheless suggests that predation is indeed a significant force structuring coral reef fish communities (Hixon 1991).

The second prediction is also supported by the results of numerous investigations. On the Great Barrier Reef, Thresher (1983a) reported a significant inverse correlation between the abundance of the piscivorous serranid *Plectropomus leopardus* and the abundance of a number of diurnal planktivores (the pomacentrid *Acanthochromis polyacanthus* and four cardinalfishes). Furthermore, over the course of a year, adult *Acanthochromis* disappeared on 3 of 4 reefs where the serranid was present, but disappeared on only 1 of 20 reefs where *Plectropomus* was absent (Thresher 1983b). In the Caribbean, Shulman et al. (1983) followed colonization of replicate artificial habitats by predator and prey fishes and found that on reefs having early immigration of snappers (*Lutjanus* spp.) subsequent colonization of grunts (*Haemulon* and *Equetus* spp.) was significantly lower than on habitats where the snappers were absent.

Hixon and Beets (1989), working in the Virgin Islands, evaluated the effects of various hole numbers and sizes on fish assemblages colonizing concrete-block reefs. They found that reefs with more holes supported more fishes and that the size of fishes on reefs was correlated to hole size (i.e. reefs with small holes supported more small fishes and reefs with large holes supported more large fishes). These results suggest that appropriate sized holes (which probably serve as refugia from predators) are an important factor in determining community structure of tropical reef fishes. During that study, Hixon and Beets also detected a significant negative correlation between the number of resident piscivores and the maximum number of potential prey fish occupying a reef, and concluded that piscivores probably set the upper limit to the number of small fishes that can occupy a reef.
Hixon and Beets (1993), again working in the Virgin Islands with concrete-block reefs, conducted manipulations designed to test a number of hypotheses regarding the role of predation in structuring reef-fish assemblages. As in their earlier investigation (1989), they 1) found a positive correlation between the number of holes available and prey abundance, although the results were complicated somewhat at higher hole densities by a temporary over-saturation of the study area with holes, and 2) they discovered that the maximum number of reef-associated prey fishes declined significantly with increasing predator abundance. Among their new discoveries, they found that prey fishes were most abundant on reefs with holes approximating their body diameter, presumably because these holes afforded maximum protection from predators. Finally, they observed a significant negative correlation between predator abundance and the maximum number of prey species observed (i.e. prey species richness), and concluded that piscivores have a negative effect on prey species diversity by nonselectively reducing and sometimes eliminating both common and rare species (see also Hixon 1991, pp 492-493).

In conclusion, predation is a process that appears to contribute to the structuring of reef fish communities by causing mortality at all stages in the life history of every fish species. According to Hixon and Beets (1993), even if fishes undergo recruitment limitation (covered next), predation can force prey fishes to compete for refuge holes and can affect local species diversity by altering the distribution and abundances of prey species.

**Recruitment Limitation Model**

The Recruitment-Limitation model, the newest and perhaps most widely accepted model, maintains that larval recruitment is usually too low for adult populations to ever reach the "carrying capacity" of the reef environment, so resources are not limiting and competitive exclusion therefor does not occur (Williams 1980, Doherty 1981, Victor 1983, Doherty and Williams 1988). A correlate to this is that population density and age structure should simply reflect variations in input of recruits, and should be not be strongly effected by postrecruitment processes like competition (Jones 1991).

Williams (1980) studied assemblages of about eight species of pomacentrid on small patch reefs in One Tree Lagoon on the Great Barrier Reef and discovered that resident populations of damselfish did not significantly affect recruitment of pomacentrids to the patch reefs. Williams found some site selection by settling juveniles, but selection was not influenced by the number of pomacentrids on the reef. He also found that over the course of the two and a half year study, the total number of pomacentrids on patch reefs fluctuated greatly. He concluded that the number of fish on any given reef was primarily dependent upon the number of larvae present in the plankton, habitat selection by larvae, and post-settlement predation, but that it was independent of competitive interactions among resident damselfishes.
Doherty (1981) questioned whether marine fishes regularly saturate reef habitats with more juvenile fishes than they can absorb thereby activating compensatory mechanisms (i.e. activating density-dependent population regulating mechanisms) whereby colonists fail to recruit to the reef or suffer high mortality after settlement. If they do, the magnitude of recruitment or the survival of post-recruitment juveniles should be inversely correlated to the density of resident adults in the habitat. In a study of the herbivorous damselfish, *Pomacentrus wardi*, on the Great Barrier Reef, Doherty (1981) compared field densities of this fish to computer-generated densities for a population based on random recruitment and density-independent mortality, and found that they could not be distinguished from each other. He concluded that this species is not normally subject to density regulation.

Victor (1983) studied recruitment and population dynamics of the bluehead wrasse (*Thalassoma bifasciatum*) in the eastern Pacific, off Panama. He was able to determine that recruitment occurs in short and sporadic episodes, in spite of the fact that adults spawn every day. Recruitment episodes of juveniles to the reef were not effected by resident wrasse densities on the reef, suggesting that competition with residents was not a factor affecting recruitment in this species. By monitoring the age structure of wrasses on a single patch reef, Victor was able to determine that the composition of the adult population directly reflected the recruitment of juveniles to the reef the year before, and was subject to dramatic fluctuations in size from year to year. He concluded that the population dynamics of the blue head wrasse were determined by the supply of recruits during the previous year and not by competition for space or some other resource on the reef.

In conclusion, coral reef fish populations as envisioned by the recruitment-limitation model are strongly influenced by fluctuations in recruitment and these fluctuations are preserved in the age structure of the populations (Doherty and Williams 1988). Larval recruitment levels are thought to be insufficient to saturate the coral reef environment, resources are never fully utilized, and competition is therefore not thought to be an important factor in regard to structuring of fish assemblages on coral reefs. In essence, density-independent and highly variable recruitment determines patterns of abundances of species and hence the population structure of assemblages of species. As summarized by Mapstone and Fowler (1988): "The species composition and relative numbers of fish present will be determined only by recruitment of planktonic larvae and larval habitat selection. Reef fish assemblages are, therefore, intrinsically very variable in space and time, with population densities and species composition being inconstant" (p. 73). For a comprehensive review of investigations supporting this model see Mapstone and Fowler (1988), Doherty and Williams (1988), and Doherty (1991).

**Summary**
Which of these models is correct remains to be determined. Although there are investigations which support each model, much current evidence supports the Recruitment Limitation Model and that model probably has the most advocates at this time (see Doherty and Williams 1988). However, Hixon (1991) makes a convincing argument that many of these models are not necessarily mutually exclusive and that there is considerable common ground for a synthesis. Nonetheless, until more work has been done, the structuring of tropical coral reef fish communities will probably remain a source of contention among ichthyologists and marine ecologists. For a recent and coordinated series of reviews of tropical reef fish community organization see Ebeling and Hixon (1991), Hixon (1991), Jones (1991), Sale (1991c), Thresher (1991), and Williams (1991).
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51


Honolulu, Hawaii


Figure 1. Summary of the life cycles of most coral reef fishes (modified from Hourigan and Reese 1987).

**Life Cycles of Coral Reef Fishes**

- **Spawning** (daily, semilunar or lunar during breeding season)
  - **Pelagic Eggs** (100->100,000)
  - **Demersal Eggs** (25-10,000)
  - **Brooded Eggs** (100->100,000)

- **Adults** (seasonal maturity in 1-5 yrs; life span = 3-20 yrs)
  - **Fertilized eggs leave the reef**
  - **Males guard the eggs**
  - **Eggs brooded orally or in pouches (usually by males) or larvae born live**

- **Juveniles** (settle onto the reef)
  - **Eggs hatch in the plankton**
  - **Eggs hatch and larvae leave the reef**

- **Larvae** (in plankton for 9-100 days)
  - **Eggs hatch/larvae leave the reef**

58