RECRUITMENT DYNAMICS OF REEF FISHES: PLANKTONIC PROCESSES, SETTLEMENT AND DEMERSAL ECOLOGIES, AND FISHERY ANALYSIS

William J. Richards and Kenyon C. Lindeman

ABSTRACT

Factors influencing variability of recruitment in coral reef fishes are of great theoretical and applied interest for population dynamics, oceanography, and fishery management. Due to the complexities of evaluating the many factors influencing recruitment processes throughout the life history of microplanktonic organisms, recruitment is often an umbrella-term encompassing interrelated problems in a management sense, but largely distinct biological processes or events. Research primarily addresses factors determining: (1) survivorship of cohorts of planktonic larvae; (2) temporal and spatial patterns of demersal settlement from the plankton; and (3) natural and fishing mortality of adult and juvenile cohorts.

Current and early research representing a variety of approaches to the recruitment dynamics of reef-associated fishes is examined. Absolute survivorship during planktonic life stages is a function of parental abundance and fecundity, and highly complex interactions among predation, oceanographic processes, growth and starvation. A matrix outlining the relative effects of important biotic and abiotic factors upon the survivorship of egg through adult life history stages is developed. Larval maneuvering behaviors which utilize specific physical features (e.g., fronts, internal waves) may be exceedingly important mechanisms for influencing transport and reducing mortality. Variability in numbers of larvae surviving through settlement can be the ultimate determinant of adult population sizes. In long-lived commercially exploited species, mortality on juvenile life stages also may significantly impact stock sizes. Variations in recruitment may also contribute to significant species composition shifts within both virgin and exploited reef fish communities.

Reef fishes are often a major component of tropical and subtropical ichthyo-faunas and support important commercial and recreational fisheries in many regions. Sound management policies are needed, but the multispecies nature of these fisheries, the complicated community ecologies of coral reef fishes, and the nearly universal pelagic dispersal of early life history stages, makes the task of understanding and modelling such systems a formidable task. Reef fishes are here considered as fishes associating with coralline or similar hard bottom environments in tropical, and to a lesser degree, temperate regions. Most reef fishes spawn externally in the water column above hard bottom structures. Fertilized zygotes subsequently undergo oceanic advection and diffusion. Even in species which guard nests of eggs or are live bearers, newly hatched larvae usually enter the pelagic realm. At the end of planktonic life, surviving larvae settle onto reefs or associated inshore environments where they mature and may eventually enter local fisheries. The importance of variable early survival of larvae upon fluctuations in adult population sizes has been recognized for many temperate marine fishes since the work of Hjort (1914; 1926). Workers in low latitudes have recently focused progressively greater attention on early life history studies, particularly processes influencing recruitment (Sale, 1980; Rothschild and Rooth, 1982).

Recruitment (in modern usage from the French “recrute” = “fresh growth” and synonymized in most dictionaries with “reinforce” or “replenish”) is often an umbrella-term for a variety of fundamental processes controlling stock maintenance. Recruitment encompasses interrelated resource management problems but highly distinct biological processes and life history stages. For example, the
term can refer to: (1) planktonic survivorship only; (2) survivorship of a cohort through planktonic and post-settlement life stages until vulnerable to a specific fishing gear; (3) the actual event of larval settlement; (4) post-settlement survivorship until initial census observation; (5) immigration of any life history stage to any new habitat/population; etc. Due to the obvious functional distinctions among these usages, the importance of clarifying the specific process or event actually under investigation should not be underemphasized (see larval settlement section for further discussion). Along with ontogenetic and discipline-specific distinctions among recruitment patterns, there are potentially major differences within and among phylogenetic levels, latitudes, and oceans. A sequentially structured framework is presented to consider three life history periods: (1) planktonic stages, (2) settlement and post-settlement stages, and (3) fishery-exploited stages. We outline and attempt to integrate the more important factors influencing reef fish recruitment processes using several approaches from marine and estuarine fishes, and planktotrophic invertebrates, from tropical and temperate regions.

**PLANKTONIC SURVIVORSHIP**

**Starvation, Predation and Growth**

High rates of mortality during the first weeks of life suggested to early workers that a “critical period” may exist within the larval stages (Fabre-Domerque and Biétry, 1897; Hjort, 1914) which can control ultimate population size. The critical period was generally assumed to occur at the time of first feeding, immediately after yolk-sac absorption. Subsequent research has failed to demonstrate a universal dependence upon the first feeding stage as the most important life history event in marine (May, 1974) and freshwater (Crowder et al., 1986) fishes. Many possible biological and physical factors (usually heterogeneously distributed) can critically affect any of several stages within the entire larval period. The relative susceptibility of the first feeding stage, and later larval stages, to starvation has been examined in many temperate fishes, often by determining the minimum feeding cessation interval required to produce irreversible starvation. The existence of “points of no return” has been both supported and contradicted among various fishes (most studies are of clupeoids, flatfish and gadoids). In most instances older larvae were significantly more resistant to irreversible starvation than younger larvae (May, 1974). There is a paucity of information on growth and starvation of reef ichthyoplankton. However, 3-week-old larvae of a temperate serranid, *Paralabrax nebulifer* showed a point of no return at 2 days and mortality at 4 days in the laboratory (Gadomski and Peterson, 1986). The impact of various suboptimal feeding regimes (continuously or discontinuously encountered) on growth and survivorship of species of subtropical sparids, engraulids and soleids has been detailed by Houde (1978) and Houde and Schekter (1978). They showed that larvae of the sparid *Archosargus rhomboidalis* apparently have less potential to be prey-limited than larvae of the engraulid *Anchoa mitchilli* and the soleid *Archirus lineatus*. Although *A. mitchilli* has the highest feeding capability, neither it nor *A. lineatus* could match the assimilation and growth efficiencies of *A. rhomboidalis*. This indicates that *A. mitchilli* larvae may maximize ingestion rate, if food is available, due to low assimilation capabilities. Such feeding strategies require denser or longer lasting food patches than those required by more efficient fishes such as *A. rhomboidalis* (an estuarine and reef perciform of the western Atlantic) (Houde and Schekter, 1978).

In marine fishes whose larvae are susceptible to reduced growth and direct or indirect mortality because of low food concentration or quality, semi-continuous
The co-occurrence of larvae with zooplankton patches may be critical. The roles of currents, wind impacts on water-mass stability, and other density-independent factors in such co-occurrence and subsequent survivorship has been emphasized in various temperate systems (Hjort, 1914; Cushing, 1977; Lasker, 1975; 1981; Peterman and Bradford, 1987). Progressive starvation can decrease searching and feeding abilities and even small changes in life stage durations due to prey-concentration and prey-quality moderated growth can lead to high magnitude increases in mortality (Houde, 1987). The interplay of density dependent and independent processes upon growth and starvation remains largely unexamined in larvae of reef fishes (Richards, 1982). These processes and the lack of basic information on larval nutritional requirements and feeding behaviors greatly limits our assessment of starvation relative to predation and other factors as determinants of successful recruitment. Two species of Gulf of Mexico sciaenids feed selectively according to the width, and perhaps swimming behavior and color of prey organisms (Govoni et al., 1986). No such studies exist for reef fish larvae. New or refined techniques for high precision analysis of nutritional status in wild-caught larvae have been developed for temperate marine fishes (Martin et al., 1985). Starvation indices can now be generated using RNA:DNA ratios, fatty acid compositions (or other histological comparisons) and morphometrics. Development and calibration of such information is needed for reef ichthyoplankton, particularly since aging of larvae using otoliths is now feasible in many reef fishes.

Invertebrate and fish predation upon cohorts of fish larvae have recently been implicated as the potentially greatest sources of mortality in marine fish larvae (Hunter, 1981; 1982; Lasker, 1981; Sissenwine, 1984). The increased interest in predation research has resulted from information on egg and yolk-sac stage mortality rates (when starvation is not a factor); laboratory and field documentation of high diversities, and generalist feeding strategies of larval and adult invertebrate or fish planktivores (see Hunter, 1981; 1982); the great array of probable predation-influenced morphological specializations of marine fish larvae (Breden, 1962; Moser, 1981); and the development of immunological techniques for analysis of predation in the field (Theilacker et al., 1986). Since invertebrate epifauna and water-column fishes of coral reefs can function as particularly high efficiency plankton filters (Hobson and Chess, 1978; Johannes, 1978), larval fish exiting or entering such communities may be exposed to very high rates of predation. Although the dynamics of predator impact have been well studied in several temperate clupeoids (northern anchovy and North Sea herring), and adult scombrids, balistids and lutjanids commonly prey upon newly-spawned labrid and scarid eggs in the Caribbean (Colin, 1982), little detailed information on prey-predator interactions in reef ichthyoplankton exists.

Predation can interact with starvation and growth when suboptimal feeding and slowed growth increases exposure of larvae to predation (Hunter, 1981). Variable rates of larval prey availability can also produce fluctuations in predator abundances (Frank and Leggett, 1985). The need for fast growth and rapid planktonic life stage transitions may be of critical importance as subtle declines in growth rates could result in order of magnitude increases in predation. Since foods are patchily distributed and each successive trophic level may have the ability to remain in such patches once found (Hunter, 1981; Harder, 1968), a cohort of larvae feeding on a dense concentration of high-quality food and therefore displaying increased growth rates, may simultaneously show decreased predation rates. Predation probably affects late-stage larvae more than starvation as older larvae are more tolerant of suboptimal feeding conditions and will eventually enter a new demersal habitat where they are exposed to many new water-column and epibenthic predators.
Dispersal, Aggregation and Retention: Oceanographic and Behavioral Determinants

Practically every important organismal-level biological factor influencing planktonic survivorship is influenced by interrelated dynamic oceanographic and meteorological processes. These processes are varied and can operate at micro- through macroscale levels (i.e., cm’s to $10^3$ km’s, following Haury et al., 1978) for reef fishes with extended larval stages. Historically, both fish and invertebrate workers have discussed possible effects of oceanographic events upon patterns of larval survival and subsequent adult population sizes (Fulton, 1897; Hjort, 1914; Johnson, 1939). A variety of physical processes can influence dispersal or retention of larval fish in both insular and continental regions (Boden, 1952; Sale, 1970; Emery, 1972; Leis and Miller, 1976; Powles, 1976; Nelson et al., 1977; Parrish et al., 1981; Shanks, 1983; Williams et al., 1984; Yoder, 1984; Norcross and Shaw, 1984; Hannan, 1984; Lobel and Robinson, 1986; Flierl and Wroblewski, 1985; Young et al., 1986; Firth et al., 1986; Bakun, in press). These studies implicate interrelated processes existing over many scales which can affect the transport field of a cohort of reef-spawned ichthyoplankton. In particular, these processes include: geostrophic and wind-influenced current regimes and related factors, such as wind-induced mixing of the surface layer, Langmuir cell convergence, or upwelling; temperature, salinity and nutrient discontinuities associated with frontal zones of gyres, eddies or coastal plumes; tidal forces; shallow-water internal waves; and bottom boundary-layer dynamics. The relative importance of a particular factor for either larval advection or retention can vary significantly between insular and continental shelf regions. For example, insular systems can be sites of a variety of vertically structured, hydrodynamically trapped oceanic features (Taylor columns—see Bakun, in press). Over most spatial scales and differing geographic regions, the most commonly encountered distribution pattern of larval invertebrates and fishes is aggregation (Haury et al., 1978; Bakun, 1986; Williams, in press). This patchiness has important implications for population and community dynamics and resource management. However, many questions regarding the relative importance of interactions among physical and biotic factors in generating and maintaining zooplankton aggregations are unsolved. Many physical features (gyres, any oceanic or shelf front, Langmuir flow) can concentrate organisms. In the remainder of this section, we discuss patterns of how reef fish adults and planktonic larvae can respond to dynamic oceanographic processes.

Reproduction.—Information on adult reproductive patterns in reef fishes is abundant relative to larval starvation, predation, and swimming behaviors. Most reef fishes are pelagic spawners and, with at least one exception, even demersal spawners have planktonic larvae (Thresher, 1984). The presence or absence of pelagic eggs and larvae in families with reef-associated species is summarized in Table 1. Spawning periodicity exists over several temporal scales in reef fishes. Many species show gonadal activity year-round with significant peaks in spring and fall (Ault and Fox, in press). Lunar periodicities exist for all moon phases, particularly the new moon in many Indo-Pacific fishes (Johannes, 1978; Lobel, 1978). Diurnal patterns also exist, with labrids, scarids and ephippids spawning during daylight (Colin, 1982; Thresher, 1984), and most other reef fishes spawning at twilight (Sale, 1980) or nocturnally. Specific patterns of spatial use during spawning also exist. Some species have mass assemblages at insular shelf edges (Johannes, 1978). Spawning rushes usually occur above high vertical-relief extensions of the reef substrata (Lobel, 1978). Robertson (1983) has demonstrated, however, that Pacific and Indian Ocean acanthurid species display considerable behavioral plasticity in both temporal and spatial patterns of spawning among different geographic
Table 1. The occurrence of pelagic eggs and larvae in families with reef-associated species whose reproduction is known: + = present, - = absent. a = gelatinous egg masses or "rafts" in some or all species; b = demersal eggs (nesters, oral brooders, or scatterers); c = live bearers. (Primary sources: Breder and Rosen, 1966; Thrasher, 1984; Moser et al., 1984)

<table>
<thead>
<tr>
<th>Family</th>
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<th>Pelagic larvae</th>
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<td>-</td>
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<td>Scorpididae</td>
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<td>+ or -</td>
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<td>Clinidae</td>
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</table>

locations. This suggests that local physical conditions may be the ultimate determinants of spawning strategies within species (McFarland and Ogden, 1985).

Many of the above patterns are believed to reduce predation on fertilized eggs in the vicinity of the original gamete cloud. There is disagreement, however, over the ultimate purposes of pelagic dispersal. Johannes (1978) argued that immediate offshore dispersal is an evolutionary response to intense predation in the adult reef habitat, and timing of spawning generally occurs during seasons of reduced
current flow or increased eddy formation to increase retention. In contrast, Barlow (1981) considered pelagic broadcasting of eggs as primarily an adaptation for dispersal because adults were distributed over widespread and patchy environments. In testing Johannes' predictions with two species of Pomacentrus damselfishes, Doherty (1983) found that hatching occurred on ebb tides and in darkness, but did not peak during seasons with reduced current flow. Based on a simulation model which incorporated patchily distributed areas of varying survival probability, Doherty et al. (1985) tested the relative success of "limited" vs. "greater" dispersal strategies and concluded that pelagic dispersal is due to selection for survival in patchy larval, not adult (after Barlow, 1981), habitats. Although the ultimate selective factors influencing dispersal probably vary in importance among taxa and regions, initial reduction of egg predation is of undisputed importance. Valuable information for these and related problems could result from comparative studies of surface structure morphology and ascent dynamics of eggs of reef fish families as Robertson (1981) has done with pelagic and deep sea fishes from northern New Zealand. The descriptive and theoretical literature on reef fish reproduction and dispersal is large and the reader is referred to references in Thresher (1984) and Doherty et al. (1985) for more detail.

**Larval Behaviors.**—Besides behaviors influencing various aspects of feeding ecology (e.g., starvation and predation), behavioral control of orientation, swimming and buoyancy are the most important biological determinants of advection or retention. Studies of reef ichthyoplankton distributions in Hawaiian (Leis and Miller, 1976; Leis, 1982; Lobel and Robinson, 1986) and Australian (Leis and Goldman, 1984; Young et al., 1986) waters have suggested the importance of larval maneuvering behaviors. A variety of complex sensory-mediated vertical movements to both maximize or minimize advection are well known in invertebrate larvae (Thorson, 1950; Strathmann, 1980; Chia et al., 1984; Scheltema, 1986). For example, larval movements in the vertical plane by Australian Penaeus shrimp can produce distributional patterns that conflict with predictions from observed oceanographic dynamics (Rothlisberg et al., 1983). Reef fish larvae, particularly after completion of caudal fin development (by 4–7 mm SL in most perciforms), should generally be capable of precise water-column maneuvering by orientation towards various cues (i.e., discontinuities in temperature, light, pressure, salinity, gravity), active swimming, and gas bladder modulation. Although such behaviors and their impact upon potential dispersal have been studied in some freshwater and temperate marine ichthyoplankton (Webb, 1975; Power, 1985), the details of these behaviors and their potential importance in reef fish larvae remain largely undocumented.

Patchiness on scales of 1 to 10's of km's can be characteristic of many temperate and tropical reef fish larvae based on water-column sampling, surveys of newly settled larvae and dispersion models (Jahn and Lavenberg, 1986; Williams, in press; Victor, 1984; Shapiro, 1983) as well as in phyto- and zooplankton (Haury et al., 1978). Such aggregations may be the result of dynamic interplay between oceanographic and behavioral processes. Physical factors influencing lateral and horizontal water movements and stratifications within the water column are probably the ultimate controls of aggregation. However, once co-occurring, planktonic taxa may exercise a variety of maneuvering behaviors to insure aggregation for feeding or other purposes. Behaviorally influenced aggregation was suggested for macroplanktonic age-0 myctophids in a field-tested advection/diffusion model developed from convergence at the ring front of a Gulf Stream warm-core ring (Olson and Backus, 1985). These authors assume vertical motions at fronts can
Table 2. Representative reef fishes, and pelagic fishes occasionally found near reefs, with specialized pelagic transformation stages (prejuvenile stages)

<table>
<thead>
<tr>
<th>Taxa</th>
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<td>Holocentridae; several genera</td>
<td>Rhynchichthys</td>
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<tr>
<td>Chaetodontidae and Scatophagidae; several genera</td>
<td>Tholichthys</td>
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<td>Mugilidae; Mugil</td>
<td>Querimana</td>
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<td>Acanthuridae; Acanthurus</td>
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<tr>
<td>Anguilliformes, Elopiformes; many genera</td>
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</tr>
<tr>
<td>Bathysaurusidae; Bathysaurus</td>
<td>Macristium</td>
</tr>
<tr>
<td>Gempylidae; several genera</td>
<td>Pax</td>
</tr>
<tr>
<td>Ipnopidae; Bathyttyphlops</td>
<td>Macristiella</td>
</tr>
</tbody>
</table>

be overcome by many zooplankters, and such species can presumably maintain an approximately constant level in the water-column. Larvae can therefore concentrate at frontal zones without expending effort on horizontally directed movements (Olson and Backus, 1985). This example of physically and behaviorally moderated aggregation may be applicable to a variety of planktonic organisms and frontal systems.

Duration of planktonic larval periods, as revealed by otolith increment analysis, varies significantly among reef fish families. Recent broad surveys of over 25 reef families reveal that larval durations for most species range between 20 and 60 days post-hatching (Brothers et al., 1983; Brothers and Thresher, 1985; Victor, 1986a). Such data provide considerable insight into dispersal abilities within and among taxa and are therefore important in ecology, zoogeography and management (Brothers and Thresher, 1985; Munro and Williams, 1985). Care must be taken, however, to insure that increment disposition is indeed daily in field-caught larvae which can encounter highly variable food concentrations and environmental conditions (Jones, 1986). Many reef and pelagic species occasionally found near reefs have prejuvenile stages with specialized morphological adaptations for extended planktonic life (Table 2). At least several of these (Acanthurus hepatus in Breder, 1949) and other species can probably delay metamorphosis and settlement after reaching an initial stage of competency. This capability is commonplace in invertebrates (Strathmann, 1978; Jackson and Strathmann, 1981; Scheltema, 1986) and may be present in larvae of many reef fish species.

SETTLEMENT ECOLOGY

The impact of influxes of new individuals to reef fish populations and subsequent implications for species coexistence and community structure has become a major focal point of population ecology. Varying arguments and evidence have been advanced regarding the roles of deterministic and stochastic processes in the structure of reef communities (Smith and Tyler, 1972; Talbot et al., 1978; Helfman, 1978; Smith, 1978; Anderson et al., 1981; Ogden and Ebersole, 1981; Sale, 1974; 1977; 1980; 1982). These papers generally emphasized either "orderly" or
"chaotic" factors in the control of community structure yet assumed that demersal resources, not supply of larvae, were limiting in most or all circumstances. These arguments have evolved to new stages as comprehensive field studies assessing larval recruitment, juvenile mortality, and adult population sizes indicate that highly variable supplies of new larval recruits control adult population sizes in damselfishes (Williams, 1980; Doherty, 1982; 1983) and wrasses (Victor, 1983; 1986b). This conclusion implies that density-independent physical factors critically affect pelagic and settlement-stage larvae. Incorporation of variable larval recruitment into recent models of the dynamics of reef and other hard-bottom marine communities (Warner and Chesson, 1985; Roughgarden et al., 1985; Underwood and Denley, 1984) substantiates the conclusions of these field studies. The demonstration of the ultimate importance of larval survival and settlement (i.e., the importance of recruitment-limitation and "supply-side ecology") on adult reef fish population dynamics parallels Hjort's (1914, 1926) original discussions of the importance of larval survival and the impact of oceanographic events in temperate regions.

Recruitment patterns of reef fishes have been documented and experimentally analyzed on a variety of temporal and spatial scales in several geographic regions. The most studies and the longest time series of available information are from regions of the Australian Great Barrier Reef, where high levels of variability in gross abundances are manifest on most scales examined (Sale, 1974; 1977; 1980; Williams, 1980; 1983; Williams and Sale, 1981; Doherty 1983; Eckert, 1984). Variation and pattern characteristic of specific scales are discussed by Munro and Williams (1985), Williams (in press), and Doherty (1987a). Major trends from these studies indicate that adult population sizes are limited by supplies of larvae and that annual variations in recruitment are explainable by very short duration (several days) settlement pulses which may occur simultaneously over tens of kilometers (Williams, in press; Doherty, 1987a). These conclusions agree with extensive studies of the bluehead wrasse on the Atlantic coast of Panama (Victor, 1983; 1984; 1986a) and demonstrate the importance of understanding physical and biological factors controlling the formation and movements of ichthyoplankton patches in regions where reefs occur. Recruitment to Hawaiian (Walsh, 1984; Schroeder, 1985) and New Zealand (Jones, 1984) reefs also shows high levels of variability and indicates supplies of larvae may limit adult populations. Cowen (1985) showed that hydrographic constraints moderate recruitment of a labrid species in areas of California and Baja Mexico where no larval sources are found upstream of the typical current direction.

Studies in St. Croix, U.S. Virgin Islands on the recruitment of several common reef species found interannual variability but not spatial variability (on the scale of 1 km); found that availability of shelter, but not food, can limit successful recruitment; and that complex interactions among juvenile and adult predators and reef-associated grazers mediates survivorship and may alter available shelter (Shulman, 1984; 1985). Highly predictable settlement pulses associated with quarter moon phases and intermediate daily tidal excursions were found for the french grunt (a haemulid) in St. Croix (McFarland et al., 1985). Notably, this species showed a short planktonic life and settlement occurred at a mean of 15 days (Brothers and McFarland, 1981; McFarland et al., 1985). Sizes of settled larvae and/or otolith studies indicate that rapid settlement (less than 20-day larval periods) typically occurs in a variety of other reef fishes. This includes at least two species of the sciaenid genus *Equetus* (Powles and Burgess, 1978), six species of the haemulid genera *Haemulon* and *Anisotremus* (Lindeman, 1986), three species of three genera of labrids (Victor, 1986a) and several genera of apogonids, po-
macentrids and pomacanthids (Brothers and Thresher, 1985). Active selection among habitats by incoming larvae can determine spatial patterns of settlement (Sale, 1980). Field studies indicate, however, that the role of this factor varies greatly among differing taxa (Sale et al., 1984; Eckert, 1985; Sweatman, 1985a). Attraction or predation by resident juveniles and adults (Sweatman, 1983; 1985b; Shulman et al., 1983) on incoming larvae may often be more important than microhabitat selection in observed distribution patterns of newly-settled individuals.

The term recruitment can have several different functional connotations. If one knows in what context the term is being used, and if the author is consistent in usage of that meaning, interpretation problems do not exist. Significant problems may arise, however, if researchers do not clearly state what life history stage or event they are actually studying. When size ranges of recruits are not stated, the terms recruitment and settlement are used interchangeably but without definition, and criteria for determining recency of settlement are not given, important questions regarding interpretation of data can arise. For example, is actual larval settlement, or interhabitat migration of already-settled juveniles, or both processes, being investigated? Many reef fishes can shift both diets (e.g., diurnal planktivory to nocturnal benthic foraging) and habitats in the first months after settlement. Uncertainty over whether different life history stages are being clustered (e.g., no distinction between 15, 70, or 150-mm recruits) limits the precision of the study. A related question is whether larval settlement, or survivorship between settlement and the first census observation, is being investigated. Keough and Downes (1982) discuss the importance of this problem in studies of larval marine invertebrate recruitment. In the burgeoning literature on reef fish recruitment, there has periodically been a lack of attention towards these and similar questions which are of fundamental importance to precise ecological analyses of early life history stages. These problems can be avoided with a brief discussion of terminology and criteria for distinguishing life history stages in the introduction or methods section of the published results. Such clarification should be a routine component of larval recruitment studies.

**REEF FISHERY RECRUITMENT**

In the analysis of fishery stocks, recruitment is often defined as "addition of new fish to the vulnerable population by growth from among smaller size categories" (Ricker, 1975). Beverton and Holt (1957) used a more elaborate definition with recruitment being the age at which fish enter the area where fishing is in progress, preceded by a pre-recruit phase from birth to recruitment age and followed by a post-recruit phase consisting of a pre-exploited phase and exploited phase. Commonly, many workers equate recruitment "to the population" with larval settlement and recruitment "to the fishery" with the numbers of each new cohort reaching the initial or the mean age (or size) of capture by a specific fishing gear. A key question in fishery management is not solely numbers spawned and surviving to recruitment but also the correspondence between adult stock size and recruitment. When adult stocks are reduced by fishing to the point that recruitment declines, recruitment overfishing has occurred (Cushing, 1973). Examples of potentially severe recruitment overfishing include both pelagic and demersal fisheries (California sardine, Peruvian anchovy, and Norwegian cod) (Garrod, 1967; Troapec et al., 1980). Identification and prevention of recruitment overfishing is difficult in temperate single-stock fisheries and extremely difficult in more complex multispecies fisheries common to many tropical and subtropical
regions (Pauly and Murphy, 1982). For example, recent dramatic recoveries of presumably overfished temperate stocks (Japanese sardine, North Sea herring) indicate collapses or explosions of some fish populations are only temporary digressions from, or returns to, long-term means (Houde, pers. comm.). In all latitudes, such management problems are largely the result of inabilities to distinguish fishery-induced fluctuations from natural variability due to physical and biological factors (Cushing, 1977; Bakun, in press).

Early analysis of stock and recruitment, developed primarily from riverine salmonid populations, emphasized that control of population sizes between generations lay in the impact of predation upon early life history stages (Ricker, 1954). In the general Ricker model, recruitment is a function of parent stock and both density dependent and independent mortality. The Ricker curve is dome-shaped with low recruitment at high, as well as low, levels of egg production. Beverton and Holt (1957) using a similar equation developed a model in which recruitment approaches a maximum asymptotically with increasing stock. Later work has incorporated random variables to approximate environmental fluctuations (Cushing, 1973; 1977). Although these basic curves and their refinements have been used in the management of some important temperate fishes (salmonoids, gadoids), they have not been shown to be appropriate in many other stocks. This is largely because most marine fishes do not possess the life history characteristics of the species these models were originally developed for. The application of temperate fishery management techniques in the analysis of lower latitude fisheries is also complicated by other factors (Pauly, 1982). These can include: (a) much higher species diversities with resultant multi-species complexities in feeding and other ecological relationships, (b) a poor understanding of stock discreteness and self-recruitment potential due to extended larval periods in many species and patchy spatial distributions of reef habitats, (c) a lack of personnel, laboratories, and adequate catch statistics due to low levels of funding and species identification problems, and (d) a lack of appropriate management models for multispecies fisheries.

A variety of techniques have been developed to analyze tropical multispecies fisheries with only marginal data available (Pauly 1982; Ingles and Pauly, 1984). By use of an empirical relationship between growth and mortality as plotted on an auximetric grid, Pauly (1980) analyzed stock and recruitment in Gulf of Thailand fisheries for Indian halibut (a pleuronectid) and false trevally (a carangid). In the trevally, plots of recruitment on spawning stock size approximated a Ricker curve and indicated recruitment overfishing. In the flatfish, however, no relationship between recruitment and parent stock size was found. This was because the flatfish was considered to be an "r-selected" species with low levels of biomass in the virgin stock. With the loss of the predatory carangid, recruitment to the stock increased greatly which allowed tolerance to heavy fishing pressure (Pauly, 1980). It has been suggested by Murphy (1982), however, that this interpretation is inaccurate due to suspect data points. The applicability of classic stock and recruitment models in tropical reef fisheries is generally limited. This is due, in part, to protracted spawning seasons and the resultant high numbers of individual cohorts quasi-continuously entering reef populations each year (Ault and Fox, in press). Further complications arise because the entrance of these cohorts into a specific reef system can be highly variable and one large settlement pulse may satisfactorily replenish an exploited stock for that year (Kami and Ikehara, 1976; Williams, in press). Due to a lack of species-level landing statistics, Munro (1983) could not assess annual recruitment of Jamaican reef fish stocks, although a recruitment index estimating the number of recruits needed to produce the ob-
served catch was calculated. In examining hook and line and trawl fisheries for reef fishes of the Atlantic coast of the southeastern U.S., Huntsman et al. (1983) concluded that stocks of serranids, lutjanids, haemulids and sparids show very similar yield per recruit models and therefore suggested all species could be managed following a single strategy. This analysis considered habitat (in contrast to Miller and Richards, 1979), not larval recruitment, as limiting. While possibly true along the outer continental shelf and slopes of Georgia through Virginia, limiting supplies of larval recruits are possibly more important in many tropical areas.

Recruitment to a fishery is a function of parent fecundity, variable mortality and growth during planktonic life history stages, loss at settlement due to inappropriate habitat and predators, and losses in subsequent post-settlement life stages prior to retention by the gear in question. In many important reef fishes (lutjanids, serranids, haemulids) several years elapse between larval settlement and fishery recruitment. Despite the greater magnitudes of planktonic mortality, early juvenile through sub-adult mortality rates can also significantly influence adult population sizes. Therefore, there is a need to precisely identify the most significant larval, juvenile, and adult life history stage transitions and eventually, age-specific growth and mortality rates for each stage. In almost all reef fishes, there are few, or no, fishery-independent estimates of these demographic variables. However, some data is now available for mortality in adult pomacanthids (Aldenhoven, 1986), and growth in juvenile pomacentrids (Ochi, 1986). Due to the high species diversities of coral reef fish communities, variability in such demographic factors (as mediated by physical or biological factors) could influence complex abundance shifts among species which are closely interrelated ecologically. Such dominance shifts are well documented in several temperate regions (Skud, 1982) and may occur in higher diversity reef fish assemblages, particularly if fishing pressure is high and supplies of larvae are highly variable for the species in question.

**DISCUSSION**

The processes influencing recruitment are confounded by interactions among both biological and physical factors. For any species, critical factors need to be monitored to predict recruitment outcomes. Most factors have their greatest impacts upon early life stages; periods when the importance of certain biological dynamics of development are easily underestimated. A major problem facing fishery managers is the need to make decisions about populations before the size of the exploited population is known or at least quite early in the exploitation process. De facto decisions may be too late, either to protect the population or to allow reasonable exploitation. The complex nature of these processes dictates that even at smaller scales of study, consideration of interdisciplinary factors is required. Determining the relative importance of individual factors and their interactions is a prerequisite for predictive modelling of recruitment. As well as providing a fundamentally important representation of the process interactions in question, graphic formalization of a conceptual model is also critical to later phases of simulation (i.e., variable and equation development, model validation and application). Conceptual recruitment models can take many graphic forms. Formalization of all models, however, requires that: (1) the essential elements of the system of interest are identified; (2) system components are categorized; and (3) essential relationships among and within systems of interest are identified. To satisfy these needs and also provide a graphically revealing framework of dynamic
processes influencing recruitment and their variations among life stages, we have organized Table 3 in the form of a two dimensional matrix. By bounding critical temporal and spatial scales of the processes under study (Bakun, 1986; Williams, in press; Doherty, 1987a) and adjusting according to available information for the population in question, this matrix can serve as a template for identifying key interactions influencing survivorship.

At the largest scales, recruitment success is a function of (1) variation in the reproductive potential of the parent stock coupled to environmental factors and (2) the survivorship of each successive life history stage as influenced by the many factors discussed earlier. There can be a highly variable mix of changing fecundity of parents, growth within each life stage per cohort, and survival within each life stage per cohort. Biotic and abiotic factors influencing annual fecundity can influence year class abundances as significantly as events affecting planktonic larvae. Despite such possibilities, individual and population-level egg production patterns are largely unstudied (with a few exception, e.g., Doherty, 1983) in low latitude reef fishes. Estimates of life stage-specific growth, starvation, and predation are largely unavailable for coral reef fishes. Additionally, identification techniques for early life stages of many reef taxa remain unavailable (Richards, 1985). Information from studies on temperate and estuarine fishes, however, when coupled with indirect evidence from coral reef fish larvae permits a general assessment of relative roles of biotic factors in recruitment. Hjort's critical period hypothesis and more recent hypotheses regarding physical processes influencing starvation mortality in first feeding larvae are probably applicable in many taxa due to patchy distributions of zooplankton prey and local hydrodynamic variability. In other life stages or transitions, starvation is probably not as important, particularly when compared to predation (Table 3). Starvation, however, also controls growth rate, which if suboptimal, can result in overwhelming mortality from both biological and physical factors. Growth remains important during older life history stages in predation minimization and egg production. Differences among species in the effects of recruitment-limitation upon stock sizes may also be influenced by growth (e.g., longer-lived fishes may be less impacted by poor recruitment years than shorter-lived species). In many species, the most important biological variable impacting demersal and, to a lesser (or equal) degree, planktonic stages, is probably mortality from predation. Along with the interaction effects among predation, growth and starvation, recruitment success is also influenced by sequences of physical entry into the system and subsequent interactions with resident fishes. The low abundances in plankton surveys of reef fish larvae relative to larvae of pelagic or midwater fishes (Richards, 1984) indicates that correlation of larval abundances with recruitment is difficult. Nonetheless, successful results have been obtained (Stevens et al., 1986). Grids of light traps may ultimately provide an optimal sampling strategy for reef ichthyoplankton (Doherty, 1987b).

The interactive roles of atmospheric and oceanic physical processes on larval distribution and survivorship have long been recognized and are now being examined in detail in several temperate regions (Lasker, 1981). Similar multidisciplinary studies of large-scale reef systems are needed. Wind effects in the surface mixed layer can greatly influence patterns of larval growth, starvation and predation. A variety of hydrodynamic processes common to continental and insular reef systems can greatly affect retention as well as dispersal. How far larvae move from the spawning site during the pelagic stage, the variance associated with this, where the larval stage is usually spent, and the geographic extent of self-recruiting populations are still largely unknown in reef fishes. The importance of larval ecological requirements for zoogeographic analysis of adult reef fish distributions
Table 3. Biological and physical factors impacting the recruitment dynamics of reef fishes predicted relative effects upon potential for cohort survivorship are represented as follows: L—large; M—moderate; S—small; N—none; U—unknown. These designations approximate order of magnitude intervals of mortality per life stage.

<table>
<thead>
<tr>
<th>Life stages</th>
<th>Biological dynamics</th>
<th>Physical dynamics</th>
<th>Oceanic</th>
<th>Water dynamics (currents, vertical shear, many others)</th>
<th>Habitat (water column or demersal)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Growth</td>
<td>Starvation</td>
<td>Predation</td>
<td>Behavioral responses</td>
<td>Disease, parasites</td>
</tr>
<tr>
<td>Egg</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nested/Brooded</td>
<td>S?</td>
<td>N</td>
<td>S-L</td>
<td>N</td>
<td>M</td>
</tr>
<tr>
<td>Planktonic</td>
<td>S?</td>
<td>N</td>
<td>L</td>
<td>N</td>
<td>U</td>
</tr>
<tr>
<td>Larva</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yolk-sac</td>
<td>M-L</td>
<td>N</td>
<td>L</td>
<td>N-S</td>
<td>U</td>
</tr>
<tr>
<td>Planktrophic*</td>
<td>L</td>
<td>L-S</td>
<td>L</td>
<td>M-L</td>
<td>U</td>
</tr>
<tr>
<td>Adult†</td>
<td>Suboptimal fecundity</td>
<td>M-S</td>
<td>S-N</td>
<td>M-L</td>
<td>M-L</td>
</tr>
</tbody>
</table>

* Some taxa have specialized (e.g., prejuvenile) life stages; see text.
† Depending on taxa, several life history stages may exist here.
has only been emphasized recently (Leis, 1986). The roles of habitat in observed patterns of distribution are also largely unknown on most scales. For example, the roles of artificial reefs in attraction (i.e., aggregation) vs. actual production (Bohnsack and Sutherland, 1985) are not well documented.

An abundance of factors, and variably complex interactions, may be present at particular scales of study. Recent empirical and theoretical information has demonstrated that reef ichthyoplankton are generally patchily distributed and limited in supply, and pulses of settlement events can radically affect individual populations (Williams, in press). Additionally, substantial changes in the size of localized populations can have significant consequences for associated species. Through "storage effects" (Warner and Chesson, 1985), species coexistence can be facilitated in periods of poor recruitment. However, dominance shifts among species may also result from variable patterns of larval recruitment (as in the sand lance, Sherman et al., 1983). The presence of recruitment driven dominance shifts in coral reef fishes has not been broadly addressed. Due to the greater diversities of fishes and ecological interactions on coral reefs, dominance shifts may not appear as dramatic as in temperate regions. Nonetheless, reef fish communities may pass through recruitment-regulated, multiple stable point assemblages as has been discussed for invertebrate fouling communities (Sutherland, 1974). Large time series of experimental and descriptive information now accumulating in certain reef areas may provide insight into this and related topics.

**ACKNOWLEDGMENTS**

We appreciate the comments of the following who reviewed drafts of this manuscript: J. S. Ault, University of Miami; B. E. Brown, Southeast Fisheries Center; P. J. Doherty, Griffith University; E. D. Houde, Chesapeake Biological Laboratory; M. F. McGowan, University of Miami; D. Y. Shapiro, University of Puerto Rico and C. L. Smith, American Museum of Natural History.

**LITERATURE CITED**


ADDRESS: National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Center, 75 Virginia Beach Drive, Miami, Florida 33149.