A key phase in the recruitment dynamics of coral reef fishes: post-settlement transition

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Synopsis

Recent studies of recruitment dynamics in demersal fishes have placed major emphasis on presettlement mortality, and little on events bridging late larval and early juvenile periods. Observations on 68 taxa of Caribbean coral reef fishes before and during settlement revealed the existence of a distinct post-settlement life phase called the transition juvenile, associated with the act of recruitment. Transition juveniles were found as solitary individuals, in conspecific groups, or in heterospecific groups. The groups were either uniform or heterogenous in appearance. The complexity of the transition phase and its apparently widespread occurrence in coral reef fishes suggests that important aspects of population structure may be determined between settlement and first appearance as a full-fledged juvenile.

Introduction

Demersal fishes in nearshore marine environments can exhibit marked year-to-year variation in local abundance, due to fluctuations in survivorship and distribution of pelagic larvae (Rothschild 1986, Bailey & Houde 1989). From a local perspective this variation has a large stochastic component, implying that presettlement mortality may be more important than post-settlement mortality in shaping the distribution, abundance, and evolutionary characteristics of demersal fish species. This view has profoundly influenced the study of the population biology of demersal fishes (e.g. Sale 1980). It is based, however, on a very limited understanding of recruitment mechanics. Very little is known about the events that take place during the ecolog-

ical phase bridging late larva and early juvenile periods (Bailey & Houde 1989), and so little importance has been ascribed to it. Organisms in this phase are referred to in the literature by a confusing variety of descriptors, including postlarvae, new recruits, settlers, late-larvae, pelagic juveniles, and juvenile recruits.

In order to proceed it is essential that we clarify our terms. We define the event of settlement as departure from the pelagic arena and adoption of life in the immediate vicinity of the benthos or other physical structure. The event of recruitment is defined as the establishment of an individual in the juvenile stock; it is the culmination of a chain of events comprising an overall recruitment process. Prior to settlement, an individual is a larva. After recruitment is completed, it is a juvenile. The ec-

ological phase between dispersal and recruitment is here referred to as the transition phase of the juvenile period. The developmental interval corresponding to this phase is referred to as the transition juvenile, or simply, the transitional.

It has recently been noted that a few species of demersal fishes pass through a distinct behavioral transition phase, during which they are present in the epibenthic environment (and therefore post-settlement by our definition), but not yet functioning as juveniles. Metamorphosis from larval to juvenile morphology does not coincide precisely with the transition phase, and may precede or post-cede it to varying degrees. Breitburg (1989) described near-bottom schooling as a 'distinct pre-settlement behavior' in what she referred to as the 'demersal larvae' of the benthic estuarine fish *Gobiosoma bosci*. Breitburg's terminology, with which we differ, is less important than her appreciation for the potential significance of this phenomenon. Breitburg cited Marliave (1986) and two personal communications comprising evidence for similar behavior among seven families of fishes on eastern Pacific temperate reefs and one in Tasmania. She postulated that interactions among schooling transitionals could influence recruitment patterns.

Victor described recruitment behavior for juveniles of the Caribbean bluehead wrasse, *Thalassoma bifasciatum*, which hides in cracks in the reef after settlement (Victor 1983, 1986a, b). He also noted that *Halichoeres bivittatus*, another Caribbean labrid, spends the first five days after settlement buried in the sand (Victor 1982). Clearly, not all demersal fishes metamorphose directly from the pelagic larval form into a full-fledged juvenile.

During July and August of 1989 we began a series of studies on the events leading up to recruitment in Caribbean coral reef fishes. In this paper we summarize patterns of larval, transitional, and juvenile behavior observed in aquaria and on the reef, mostly during a 10 day saturation dive. Quantitative light and suction trap sampling experiments on midwater larvae were conducted concurrently with these observations, with results to be published separately. To date, our findings indicate that hiding in cracks, diving into the sand, and schooling near the bottom (Victor 1982, 1983, Breitburg 1989) are but three examples of a widespread and richly varied phenomenon among fishes with pelagic larvae: a life phase corresponding to the actual process of recruitment, during which individuals may exhibit behavioral and morphological specializations which facilitate the transition between the pelagic and the demersal ways of life.

Methods

The observations presented here were made at two Caribbean locations during the 1989 summer field season: the Discovery Bay Marine Laboratory and the north-central coast of Jamaica; and in Salt River Canyon, St. Croix, U.S. Virgin Islands. In Jamaica, settlement phase larvae were obtained by sweeping handnets beneath floating nightlights powered by 12V automobile batteries. These specimens were transported in buckets to the laboratory, and placed in aerated 40 liter all-glass aquaria for observation. Transition juveniles were observed on the reef, and some were collected with handnets for further observation in aquaria. Representatives of species marked by an asterisk in Table 1 were airfreighted in early life stages to the New England Aquarium for rearing and subsequent use in research and public display.

Data from St. Croix were obtained during a 10 day saturation mission in the National Underwater Research Center's AQUARIUS Habitat (the Salt River Canyon environments and fish assemblages are described in Kaufman & Ebersole 1984). The appearance and behavior of larvae, transitionals, and recruits were observed on the reef by day and by night, around the exterior of the Habitat, and at minireefs constructed by arranging corals, rubble, and sand on sills outside the large viewing ports on the bow and port sides of the Habitat. Additional larvae were captured at night by sweeping handnets beneath the Habitat floodlights. These were maintained and observed within the Habitat in aerated 40 l aquaria. Four presence/absence censuses for transitionals and recruits were conducted between 16 and 30 m depth in each of two microhabitats, vertical wall and gorgonian flat, following the

methods of Kaufman & Ebersole (1984). Two reconnaissance excursions to 45 m depth (of 90 minute and 45 minute durations) were made to assess presence/absence of transitionals and recruits unique to deep reef slope environments.

Results

Sixty-eight species were observed as settlement-size larvae, transition juveniles, or recent recruits (Table 1). Our observations indicate that the transition phase is a prolonged process, and that transition juveniles have distinct functional characteristics. Duration of the transition phase ranged from hours to weeks according to species, but this could be a plastic character. For example, several hundred juvenile *Clepticus parrai* were observed during the mission in size-graded schools, mostly over coral pinnacles at 20 to 30 m. Recently settled individuals were transparent, often mixed with transparent transitionals of other species, while juveniles are pink-violet. Onset of juvenile coloration was manifested over sizes ranging from approximately 1 to 3 cm.

All specimens caught in the water column at night, away from the reef, were considered pelagic larvae. Pelagic larvae were predominantly transparent or silvery, with visible and characteristic melanophore patterns (Leis & Rennis 1983, Leis & Trnski 1989). On three successive nights of observations from the Habitat ports, we saw gigantic (8 cm SL) *Acanthurus* sp. larvae, most likely *A. coeruleus*, that appeared to be different individuals, alongside settling stage congenerics one fourth their size.

Pelagic fish larvae appeared around the Habitat ports in large numbers beginning about one hour after darkness. Those marked 'MS' (mast settlement) in Table 1 gathered heavily around the ports in pulses lasting 30 to 60 minutes. One settlement and transition event was observed for *Canthigaster rostrata* from the Aquarius ports. Our interpretations are limited by the field of view of the port, but this individual appeared capable of reversing part of the settlement process to return to the water column. Three pelagic phase individuals were observed at night near the Habitat floodlights. All were inflated, golden balls. One was observed to deflate into a miniature in form and color of the juvenile, and then, within only a few minutes, to reverse this process and rise again into the water column. A single individual each of transition phase *Sparisoma* spp., *Monocanthus tuckeri*, and *Synodus intermedius* were also seen to change color and apparently return to the water column after settling on the windowsill of the habitat for from 4 to 20 hours. These and other species of further families (Synodontidae, Tripterygiidae, Labridae, Apogonidae) moved about or rested in contact with the minireef or windowsill for several minutes to as long as one day. Then they either entered the water column or moved elsewhere in the vicinity of the habitat. It is uncertain to what extent the behavior of these individuals, once settled, might have been influenced by the floodlights.

Specimens observed settling in aquaria, or in close association with the reef, were considered transition juveniles unless they exhibited the coloration and behavior characteristic of well-established juveniles. Transition juveniles were either transparent or vividly colored, but were often distinctly different in both appearance and behavior than the juveniles of their species. Several of the species observed as settlement phase larvae exhibited morphology that was intermediate between a distinctive larva form and the post-recruitment juvenile condition (e.g., *Holocentrus pocos, Dactylopterus volitans, Synodus intermedius, Pseudopeneus mulloidichthys*).

The two deeper reconnaissance dives to 45 meters below the surface added no new species to those regularly observed between 18 and 30 meters, where the majority of observations were made.

The most easily observed transition phase juveniles were those that assembled in groups. In some cases the groups were loose aggregates; in others, schools of either similar-sized or size-graded individuals. The groupings could be either conspecific or heterospecific. If the latter, we termed it either 'uniform', indicating that several species which aggregated together were hard for an observer to distinguish, or 'heterogeneous', in which case a human observer found the aggregated species to be

Table 1. Observations on early life stages of coral reef fishes during July-August 1989 at Discovery Bay, Jamaica and Salt River Canyon, St. Croix, U.S. Virgin Islands.

Intervals observed: L – pelagic larva; TJ – transition juvenile; SJ – small juvenile, fully metamorphosed. Species marked with an asterisk were observed undergoing metamorphosis in an aquarium or on experimental substrata placed on the Aquarius port sills.

Where observed: AF – Aquarius floodlight; MR – Aquarius sill 'minireefs'; SS – settlement survey; NDB – sea surface nightlight, Discovery Bay, Jamaica; DB – daytime, west fore-reef slope, Discovery Bay at 15 to 20 m depth.

Strategy: MS = mast settlement; CRYP = cryptic; HS = habitat specific (HS* = often in groups of 2 to 3); CUS = conspecific uniform size; CMS = conspecific mixed size; HUG = heterospecific uniform grouping; HHG = heterospecific heterogeneous grouping.

Taxa observed	Intervals	Where	Strategy
Megalopidae	L	NDB, AF	MS
Anguilliformes			
Anguilliformes sp.	L	NDB	?
Nystactichthys halis	SJ	SS	CMS
Synodontidae			
* *Synodontus intermedius*	L, TJ, SJ	NDB, MR, SS	MS, HS
Synodontus spp.	L	AF	MS
Clupeidae			
Jenkinsia lamprotaenia	L, TJ, SJ	NDB, AF, SS	MS, CUS
Holocentridae			
* *Holocentrus pocos* (?)	L, TJ	NDB	CRYP
Polynemidae			
* *Polydactylus* sp.	L, TJ, SJ	NDB	MS
Serranidae			
Serranus tabaccarius	TJ, SJ	AF, SS	HS*
Serranus tigrinus	SJ	SS	HS
Serranus tortugarum	SJ	DB	CMS
Serranus baldwini	SJ	SS	HS
Schultzea beta	TJ, SJ	SS	HUG
Parasphyraenops incisus	TJ, SJ	SS	HUG
Grammidae			
Gramma loreto	SJ	SS	CMS
Apogonidae			
* *Apogon townsendi*	TJ, SJ	SS, AF, MR	CMS
Apogon lachneri	SJ	SS	CMS
Phaeoptyx pygmentarium	SJ	SS	HS
Carangidae			
Caranx latus	TJ	AF	CUS
Decapterus sp.	TJ, SJ	AF, SS	CUS
* *Selene vomer*	L, TJ	AF	CUS
Scombridae			
Scombridae sp.	L	AF	?
Gempylidae			
Promethichthys prometheus	L	NDB	?
Lutjanidae			
* *Lutjanus synagris*	L, TJ, SJ	SS, AF	HS*
Lutjanus buccanella	SJ	SS	HS*
* *Ocyurus chrysura*	L, TJ, SJ	SS, AF	HS*

Taxa observed	Intervals	Where	Strategy
Haemulidae			
Haemulon spp.	TJ	SS	HUG
Haemulon flavolineatum	TJ, SJ	SS	HUG
Haemulon aurolineatum	TJ, SJ	SS	HUG
Haemulon striatum	TJ, SJ	SS	HUG
Inermiidae			
Inermia vittata	TJ, SJ	SS	HUG
Sciaenidae			
Equetus punctatus	TJ, SJ	DB	HS*
Mullidae			
* *Pseudopeneus mulloidichthys*	L, TJ, SJ	NDB	HS?
Pomacentridae			
* *Stegastes leucostictus*	L, TJ, SJ	NDB, DB	HS
* *Stegastes partitus*	L, TJ, SJ	NDB, SS, AF	HS*
* *Stegastes variabilis*	L, TJ, SJ	NDB, SS	HS
* *Stegastes planifrons*	L, TJ, SJ	NDB, SS	HS
Chromis insolatus	TJ, SJ	SS, DB	HHG
* *Chromis enchrysura*	L, TJ	NDB	?
Chromis multilineata	TJ, SJ	SS, DB	HHG
* *Chromis cyanea*	TJ, SJ	SS, DB	CUS
Labridae			
Halichoeres garnoti	TJ, SJ	SS, DB	HHG
Halichoeres pictus	TJ, SJ	SS, DB	HHG
Halichoeres bivittatus	TJ, SJ	SS	HS
Bodianus rufus	TJ, SJ	SS, MR	HHG
* *Clepticus parrai*	L, TJ, SJ	SS, DB, MR	HUG
Thalassoma bifasciatum	SJ	SS, DB	CRYP/HS*
Cryptotomus roseus	TJ, SJ	SS, AF, MR	HS*
Sparisoma aurofrenatum	SJ	SS	HS*
Sparisoma viride	TJ, SJ	SS, MR	HS/HHG
Sparisoma rubripinne	SJ	SS	HS
Scarus taeniopterus	TJ, SJ	SS	HS/HHG
Sphyraenidae			
Sphyraena barracuda	L, TJ, SJ	AF, NDB	HS?
Gobeisocidae			
* *Gobeisox* sp. (?)	L, TJ	SS	HS?
Gobiidae			
Coryphopterus personatus	TJ, SJ	SS	CUS
Coryphopterus glaucofraenum	SJ	SS	HS/CMS
Coryphopterus lipernes	SJ	SS	HS/CMS
Gnatholepis thompsoni	SJ	SS	HS/CMS
* *Gobiosoma evelynae*	SJ	SS, MR	HS/CMS
Risor ruber	SJ	SS	HS/CMS
Microdesmidae			
Ioglossus hellenae	SJ	SS	CMS
Dactylopteridae			
* *Dactylopterus volitans*	L, TJ, SJ	NDB	HS?
Scorpaenidae			
Scorpaena inermis	SJ	SS	HS
Acanthuridae			
Acanthurus spp.	L	AF	?
* *Acanthurus bahianus*	L, TJ, SJ	NDB	HS?
Tetraodontidae			
* *Canthigaster rostrata*	L, TJ, SJ	SS, MR	HS
Alutera scripta	L	AF	HS
* *Monocanthus tuckeri*	L, TJ, SJ	AF	HS

markedly different in appearance. This distinction was made because of the possibility that 'uniform' groups were functioning as interspecific mimics, as opposed to the unlikelihood of such a possibility in the heterogeneous groups. The behavior patterns associated with settlement and recruitment for the observed species were assignable to one of six generalized patterns, described below.

1. Cryptic pattern (CRYP). Species with cryptic transitionals not visible on the reef and were rare in samples, but could be observed if caught as larvae in the plankton and allowed to metamorphose in an aquarium. The two species in this category that we observed in this way retained aspects of the pelagic larval form upon settlement, but exhibited characteristic coloration and behavior. The holocentrid still bore the characteristic cephalic helmet and rostral spike 21 days after capture, which was 19 days after settlement and the assumption of a benthic-cryptic behavior and a red, black and white color pattern. The settlement phase *Dactylopterus volitans* continued to lose head spination after assuming demersal habits and transitional (silver, black, and white) coloration in an aquarium.

2. Habitat specific (HS). This pattern was observed in at least 31 species. The transitionals were encountered post-settlement as individuals within a particular substratum type or macrohabitat. In Table 1, the 9 species in this category marked by an asterisk (HS*) are those which were frequently present in loose groups consisting of 2 or 3 conspecifics. The HS pattern was exhibited by all three of the Tetraodontiformes we observed.

3. Conspecific uniform size (CUS). Observed here in 6 species, CUS is characterized by aggregates, presumably representing a recruitment pulse of non-related individuals, approximately uniform in size. Sometimes several size classes are present in close proximity within the context of a continuous, size-graded aggregation. CUS groupings were not closely associated with other species, or only indifferently so. Species with demersal juveniles exhibited a brief transition phase distinct in coloration and behavior (e.g., *Polydactylus oligodon* (?), *Pseudopeneus maculatus*, *Stegastes* spp., and *Chromis* spp.).

4. Conspecific mixed size (CMS). Very small juve-niles observed in close association with conspecifics of varied sizes. In 5 of the 11 cases it could not be determined if the pattern resulted from the presence of conspecifics, or from appropriate habitat in which conspecifics just happened to occur.

5. Heterospecific uniform grouping (HUG). Seven species of transition phase juveniles were observed in conspecific clusters amid larger groups of visually and behaviorally similar individuals of other species. This was the most striking of the aggregate patterns we observed. HUG transitionals exhibited little change in morphology or coloration as they settled, but did change markedly in behavior. For example, the midwater planktivores *Clepticus parrai, Inermia vittata, Haemulon striatum, Schultzea beta,* and *Parasphyraenops incisus* were all transparent or nearly so as settlement phase larvae. Upon settlement, they remained nearly transparent, but switched from an unknown but presumably free-swimming pelagic behavior to foraging in tight monospecific compartments within larger heterospecific foraging clouds. These miniature planktivore clouds massed over coral pinnacles at depths of 10 to 40 meters.

Most of these species exhibited morphological convergence for terete form and/or caudal fin forking. A second example of the HUG pattern was illustrated by heterospecific aggregations of *Haemulon* spp., observed grouping alongside *Heteromysis* swarms over *Halophila* beds in the center of Salt River Canyon, as reported by MacFarland et al. (1985). During our study period these aggregates were dominated by *H. flavolineatum* and *H. aurolineatum.*

6. Heterospecific heterogeneous grouping (HHG). The 6 species exhibiting HHG settled with a juvenile form, but exhibited distinct coloration and/or behavior. They were observed individually or in conspecific clusters amid larger groups of visually and behaviorally dissimilar species. HHG is apparently a prevalent strategy in the Labridae (including both wrasses and parrotfishes, sensu Kaufman & Liem 1982). We frequently observed transition phase labrids in heterospecific foraging groups.

Discussion

Most of the literature on marine fish recruitment suggests that the process is fast and direct, like a parachute drop. The complex larval transformations familiar from both pelagic (e.g. *Luvarus*, Johnson 1989), and coral reef fishes have generally been associated with the pelagic ecology of the larva period. Events transpiring between the onset of settling competence and actual recruitment have been obscure, as were the functional relevance of late larval coloration, morphology, or behavior to recruitment dynamics.

The first sign of deficiencies in this view was the discovery that both invertebrate and fish larvae are capable of delaying settlement for days or weeks after settlement competence has been achieved (Randall 1961, Pearcy et al. 1977, Jackson & Strathmann 1981, Victor 1986a, b). This was evidenced in our own observations of unusually large acanthurid larvae (8 cm SL) near the Habitat. Thus, the pelagic or pre-settlement portion of the transition window is not instantaneous: once they have achieved settling competence, the larvae of some species still have days or weeks before they must settle.

Victor (1983) found reduced growth rates in *Thalassoma bifasciatum* as they entered the pelagic settlement phase, and postulated that this might be due to 'a shift in behavioral repertoire from one that maximizes food intake and minimizes predation to one maximizing the chance of return to coastal waters...'. Kendall et al. (1984) noted that 'In several groups, where the transformation stage is prolonged, the fish have developed specializations that are distinct from both the larvae and juveniles'. It appears from context that Kendall et al. (1984) assumed all such forms to be pelagic. They cited the silvery herring-like neustonic settlement phases of *Urophycis*, *Holocentrus*, mullids, mugilids, and some scorpaeniformes; other examples include the cheilodactylid 'paperfish' larva (Allen & Heemstra 1976), the giant late-stage larvae of certain flatfishes (Ahlstrom et al. 1984, Amaoka 1972, Barham 1966, Heemstra personal communication) and *Polydactylus oligodon* (?) (this paper).

Our observations support Leis' (1991) statement that recruitment can be a prolonged and richly varied process. The post-settlement or transition phase of recruitment can be only hours or minutes long in some pomacentrids (e.g., the *Stegastes* spp. we observed), or at least three weeks, as in the holocentrid. Leis (1991) also discussed the highly variable relationship between metamorphosis and settlement, and reviewed examples of complex transition behavior, including settlement into intermediate habitats, presettlement, and bouncing, or reentry into the water column. The potential duration and complexity of the transition phase supports suggestions that predation (Sissenwine 1984, Bailey & Houde 1989), interactions among transitionals (Breitburg 1989), and interactions between transitionals and established individuals (Shulman et al. 1983, Stimson 1990) can all impact distribution and abundance patterns.

We are not the first to recognize the existence of a distinct transition phase, but its importance as a widespread, general phenomenon has been underappreciated. The uniform group patterns, both conspecific (CUS) and heterospecific (HUG), appear analogous to Breitburg's (1989) 'demersal schooling larva' in *Gobiosoma bosci*. In addition to the work of Breitburg (1989), Marliave (1986) and Victor (1986a, b) there are examples of apparent transitional behavior scattered throughout the literature. Robertson (1975) described a 'benthic larva' or tenuis interval in carapids; Tanase & Arage (1975) noted that anemonefishes were dark in color and benthic for several days before assuming the coloration and symbiotic behavior of the juveniles.

One matter worth further investigation is whether fully pelagic species have a transition phase. We observed transition characteristics for several reef fishes that are at least semi-pelagic as established juveniles (e.g. *Jenkinsia lamprotaenia*, *Schultzea beta*, *Parasphyraenops incisus*, Carangidae, *Ocyurus chrysura*, *Inermia vittata*, *Chromis cyanea*, *Clepticus parrai*). The difference in process between a shift from pelagic larva to the shelter of the seabottom and a shift to the shelter of a school could be mostly semantic.

The fact that so many species do exhibit a transition phase clearly indicates that settlement and

recruitment are often separate events. The overall recruitment process for most demersal marine fishes consists of a pelagic and a demersal phase, each with its own potential for developmental plasticity.

Our terminology differs from that of previous authors, whose definitions have usually excluded ecological function or behavior and coloration as considerations. Hubbs (1943, 1958) and Lewis et al. (1972) used the term 'prejuvenile', while Balon (1985) found the menhaden prejuvenile of Lewis et al. (1972) to be the actual metamorphosis, 'prolonged into a separate step – a precarious and little understood homeorhetic state'. Balon (1985) also emphasized the importance of recognizing that not all fishes undergo a pronounced metamorphosis. Leis & Rennis (1983) condemned the use of 'prolarva', 'postlarva', 'protopterygiolarva', 'prejuvenile', and like terms as being either etymologically contradictory or simply unclear. We suspect that Hubbs' prejuvenile and Leis & Rennis' (1983) settlement juvenile refer to our settlement phase. Leis (1991) considered settlement synonymous with the ecological transition from open water to benthic environments. Marliave (1986) and Breitburg (1989) were probably the first to document clear examples of the transition phase defined here.

Recognizing transition phase juveniles in preserved samples would be difficult for most species because it is coloration and function, rather than morphology, that is most distinct about the transition juveniles we observed. Further studies are needed to assess the importance of morphological characteristics unique to the transition phase. Despite their varied characteristics we anticipate that patterns in functional morphology for the transition phase will correspond in a meaningful way to different patterns of recruitment-associated behavior, such as the six that we happened to observe during our study. For example, the terete, streamlined form of HUG transitionals is probably the result of selection for their trophic role as station-holding planktivores. This form is extremely common among early juveniles of many percoid families (Johnson 1984), suggesting that demersal schooling might prove to be even more widespread than we have proposed.

It is possible that functional convergence among

transition juveniles can also result from selection for mimicry, i.e., mimicry can become the recruitment strategy. In the Indo-Pacific, at least three species exhibit an extreme form of CUS characterized by extended parental care, brief or nonexistent pelagic phase, and a transition phase with distinct coloration and behavior. *Plotosus anguilliaris* deposits large eggs, producing fully-formed, aposematically colored, and highly venomous transitionals that aggregate and condense into a tight ball when disturbed. *Pholidichthyes leucotaenia* emerge from their parents' burrows as transitionals which apparently mimic *P. anguilliaris* swarms in coloration and behavior. Another important aspect of CUS is the potential degree of genetic relatedness among members of an aggregate. In *P. anguilliaris*, *P. leucotaenia*, and the pomacentrid *Acanthochromis polyacanthus* (which exhibits extended parental care), transition aggregates are likely to result from only one or a few pairings (Leis & Trnski 1989, Thresher 1984, Robertson 1973, Kaufman personal observations). There is some evidence that other marine fishes lacking a true larval or pelagic phase exhibit similar behavior (e.g., Brotulidae; Longley & Hildebrand 1941).

Some patterns of transitional behavior mirror relationships commonly seen among established juveniles and adults, except that they include species which in later life behave in an entirely different fashion. The HHG pattern we observed was a miniaturized version (most individuals in these groups were only about 1.0 to 1.5 cm in length) of the heterospecific foraging groups so familiar for larger, juvenile and adult labrids (Itzkowitz 1977, Wolf 1983, 1987). We frequently observed transitional *Halichoeres pictus* and *Bodianus rufus* in close association with each other and with larger benthic foraging groups. As adults, however, they differ: *H. pictus* aggregates in midwater to feed on near-reef plankton, while *B. rufus* becomes solitary, passes through a phase as an ectoparasite-picker, and ends up a benthic durophage.

It is possible that a transitional phase could be shortened or entirely eliminated by better preparing the larva for direct recruitment. The three tetraodontiforms we observed seemed to accomplish this by reaching a large size and advanced stage of

development prior to settlement. Such individuals have previously been referred to as pelagic juveniles (Leis & Trnski 1989, Thresher 1984, Leis & Rennis 1983, Randall & Klausewitz 1973, Randall 1971). Pelagic juveniles can be very large; Leis (1978) reported a 180 mm *Diodon hystrix*. The term 'juvenile' is appropriate here if one adopts the alternative interpretation that the transitional phase in these species is actually very long, but happens not to be spent on the reef. Instead, it is usually in association with pelagic substrata such as floating macrophytes or jellyfishes (Leis 1991). This is no different than the pattern of initial settlement into a non-adult nursery habitat, again a common pattern among tetraodontiforms (Thresher 1984) as well as many other families (Randall & Randall 1961, Leis 1991).

Many species readily observed as transitionals by catching larvae at nightlights and watching them metamorphose in aquaria, are rarely if ever seen in this phase on the reef. These species, including the tiny holocentrid and dactylopterid that we observed, are most likely cryptic. Crypsis on settlement was similarly postulated for epinephelline serranids (Thresher 1984), and has been described for sciaenids (Powles & Burgess 1978) and labrids (Victor 1982, 1986a, b). It is likely that transition juveniles of a large number of coral fishes are unknown because they are cryptic, hiding in the sand, amongst rubble, or deep within the voluminous inner spaces of coral and rocky reefs, inaccessible to either visual observation or collection. Extensive work in aquaria with settlement phase or propagated stock is needed to explore this possibility.

For those species in which the transition phase plays a major role in recruitment, there could be important population consequences. Behavioral flexibility during transition could amplify adult-juvenile interactions by providing greater opportunity for avoidance of established conspecifics (see Stimson 1990). Density-dependent effects could arise in the case of group recruitment strategies. The effects of a good larval set on overall recruitment success could be greatly amplified by nonlinear improvements in transitional survival through predator swamping and selfish herd defense. Below a certain density threshold, the effect could

work in the opposite direction, resulting in an extremely poor recruitment success. If any such nonlinear relationships are found, it will indicate that the specializations of the settlement and transition phases can reduce the uncertainty of mortality processes during recruitment, making it considerably less of a crap game than has been imagined (Sale 1978). Though settlement remains something of a suicide drop, the transition phase which follows is apparently a long, dangerous glide through a series of difficult, but predictable challenges.

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