Roles of Behavioral and Physical Factors in Larval and Juvenile Fish Recruitment to Estuarine Nursery Areas

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Abstract.—Recruitment to and maintenance in estuaries are important parts of the early life history of many fish species. Field studies have documented patterns of estuarine recruitment for several species; although some studies have postulated passive mechanisms for recruitment, the majority suggest specific behavior patterns that clearly correlate with physical factors or other stimuli. We consider recruitment to the estuary of species spawned offshore as a two-stage process dependent first upon factors in the offshore planktonic environment and second upon estuarine factors related to tidal flux. Rather than a simple stimulus–response mechanism related to a single physical factor, we suggest that the suite of factors associated with tidal flux at particular locations may act as the zeitgeber for an endogenous rhythm with a tidal periodicity. In this manner, an animal may use tidal-stream transport both for movement into the estuary and for maintenance within the estuary. Further work in the laboratory is necessary to elucidate these behaviors in fishes, particularly those related to endogenous rhythms and the stimuli that serve as zeitgebers.

Use of estuarine nursery areas is an important phase of the life history of many marine organisms, including many commercially valuable shrimps and fishes (McHugh 1967; Staples 1980; Haedrich 1983). The net seaward movement of estuarine waters, combined with tidal flux, causes problems for taxa using estuaries; these problems are generally related to either export from or recruitment to the estuary. Different strategies of estuarine use are apparent among taxa. Several species are resident in estuaries throughout their life histories. Their primary recruitment problem is to prevent the export of early life history stages from the estuary (Johnson and Gonor 1982), and they often solve this by producing large, demersal eggs (Hempel 1979) and having brief larval stages. Species that visit periodically as adults for feeding or spawning face the problem of locating the estuary; if they spawn there, their larvae face the same export problems as the residents. The interactions between hydrographic features of an estuary and population maintenance have traditionally fascinated biologists. Early interest centered upon the ability of planktonic organisms, including larvae, to remain in estuarine systems despite tidal flushing (Rogers 1940; Carriker 1951; Bousfield 1955). Early hypotheses explaining retention in estuaries generally invoked the use by organisms of the net landward flow in the deeper waters of stratified estuaries. Rogers (1940), for example, suggested that larvae of rainbow smelt *Osmerus mordax* were retained in a stratified estuary through a mechanism of vertical migration, but were transported out of the system in another, intensively flushed, estuary. Thus, specific behavior patterns and estuarine hydrography may interact to retain larvae or plankton within estuaries. The hypothesis of vertical migration based upon a tidal rhythm (shallow at flood, deep at ebb) suggested by Carriker (1951) has been confirmed by Cronin and Forward (1979) for larvae of the crab *Rhithropanopeus harrisii*.

Among the least understood mechanisms of transport associated with estuaries is the one used by species that spawn offshore and subsequently enter estuarine systems as late larvae or early juveniles. These larvae must first move to nearshore areas, then locate an estuary mouth, and finally move into the estuary. This phenomenon is related to, but distinct from, retention in estuaries; it depends upon physical factors but is linked to active behavioral responses on the part of larvae. Movements to the nearshore environment from offshore are generally considered to be either passive or some form of modulated transport; in the latter case, behavioral attributes such as vertical migration or residence in convergences associated with internal waves play a role in movement (Shanks 1983; Kingsford and Choate 1986). Fishes spawning in the same offshore habitat may ultimately have different larval distributions, suggesting that small behavioral differences among species may alter susceptibility to passive transport (Powles 1981). The groups using estuaries typically are transported by drift to the nearshore environment (Rothlisberg et al. 1983; Miller et al. 1984; Boehlert and Mundy 1987). Nelson et al. (1977), for example, suggested that wind-driven Ekman transport is the mechanism of movement to the nearshore area, and that interannual variability in transport ultimately leads to variation in year-class strength.

Although movement to nearshore areas may be passive, the overwhelming evidence from both experimental and field work is that immigration of early life stages into the estuary is an active behavioral process. Such evidence exists for a variety of fish families, including anguillids (Creutzberg 1961; McCleave and Kleckner 1982), sparids (Pollock et al. 1983; Tanaka 1985), sciaenids (Weinstein et al. 1980), bothids (Weinstein et al. 1980), pleuronectids (Creutzberg et al. 1978; Tsuruta 1978; Rijnsdorp et al. 1985; Boehlert and Mundy 1987), and albulids (Pfeiler 1984). Still, the behavioral responses to physical factors influencing estuarine recruitment are poorly understood for the majority of taxa. In this paper, we consider the evidence for behaviorally mediated entry into estuarine nursery areas as a function of physical factors.

Physical Factors Influencing Estuarine Recruitment

We recognize two major phases of movement necessary for recruitment to estuaries by species spawned offshore. The first is accumulation of larvae in the nearshore or coastal zone as described for Atlantic coast fishes by Nelson et al. (1977) and Miller et al. (1984); the second is the process of accumulation near inlets and estuary mouths and eventual passage through them. Each process involves a distinct set of physical factors to which the larvae respond and thus a distinct set of behaviors needed by the larvae to reach their optimum environment.

Nearshore Accumulation

Accumulation in the nearshore zone is essentially passive, because larvae at this stage are typically planktonic; directed vertical movements, however, may modulate this transport to maximize shoreward movement. Accumulation can be prolonged, because many species are near ages of 60–90 d when immigration to estuaries occurs (Rosenberg 1982; Miller et al. 1984), and the youngest larvae are generally found most distant from the nearshore zone (Miller et al. 1984). Behaviors associated with shoreward movement are likely related to distribution in the water column and have evolved to take advantage of mean current conditions in the species' habitat. Behavioral differences between species can result in different distributions. Richardson and Pearcy (1977), for example, described coastal (0–28 km) and offshore (beyond 28 km) assemblages of ichthyoplankton that are persistent from year to year along the Oregon coast. Many species in the offshore assemblage are spawned along the coast, in some cases in the same season as species that remain in the nearshore assemblage. The species within these two groups show clear differences in their use of estuaries (Table 1). Thus, passive movements by larvae must be modulated by a behavioral component that, under mean conditions, results in the observed distributions.

Surface drift has been implicated in many studies of planktonic distribution, but the evidence from larval distributions is not always clear. The physical environment of the Atlantic menhaden *Brevoortia tyrannus,* including the surface and bottom currents, was investigated in the Chesapeake Bight by Harrison et al. (1967), who concluded that benthic orientation of larvae and their occurrence in deep water could result in passive transport to the mouth of Chesapeake Bay. Nelson et al. (1977), however, suggested that surface drift from Ekman transport was the operating transport mechanism. Later studies suggested an even more complex picture; Miller et al. (1984) proposed that both surface and bottom waters move offshore in winter months but that midlevel waters move onshore. Abundance of Atlantic menhaden larvae does not differ between deep and shallow water (Kendall and Reintjes 1975); thus a midwater distribution and avoidance of the surface and bottom offshore transport layers may result in onshore transport.

Other evidence exists for the importance of surface water transport. Early life stages of the English sole *Parophrys vetulus,* one of the few fish species on the west coast of North America that spawns offshore and uses estuaries as nursery grounds (Krygier and Pearcy 1986), are members of the nearshore ichthyoplankton assemblage (Richardson and Pearcy 1977; Mundy 1984). Recruitment to estuaries occurs on night flood tides for fish already beginning morphological transformation. A negative correlation exists between recruitment pulses of early stage larvae and the upwelling index (Figure 1). Larvae in early stages of transformation typically enter the estuary throughout the water column, whereas later-stage larvae arrive deeper in the water column. The correlation with the upwelling index is strong for

TABLE 1.—Selected species of fish larvae collected in abundance from Oregon marine waters (Richardson and Pearcy 1977), classified by distribution, by abundance in Yaquina Bay, Oregon, and by stage of development when found in the bay. Asterisks indicate species using the bay as a nursery. Distribution categories were modified from Richardson and Pearcy (1977); taxa categorized as "bay" include those found to be abundant by Pearcy and Myers (1974) and Mundy and Boehlert (unpublished data).

Distribution	Abundance in Yaquina Bay	Species	Developmental stage in Yaquina Bay
Offshore	Absent	*Tarletonbeania crenularis*	
		Microstomus pacificus	
	Rare	*Engraulis mordax*	Postflexion
		Stenobrachius leucopsarus	Preflexion
		Glyptocephalus zachirus	Preflexion
	Common	*Sebastes* spp.	Preflexion
Offshore and coastal	Common	*Hemilepidotus hemilepidotus*	Preflexion
Coastal	Absent	*Radulinus asprellus*	Preflexion
	Rare	*Microgadus proximus*	Preflexion, flexion
		Isopsetta isolepis	Preflexion
		Platichthys stellatus	Pre- to postflexion
	Common	*Clinocottus acuticeps*	Pre- to postflexion
		Psettichthys melanostictus	Postflexion
	Abundant	*Clupea harengus pallasi**	Pre- to postflexion
		Osmeridae	Pre- to postflexion
		Anoplarchus spp.*	Pre- to postflexion
		Pholis spp.*	Pre- to postflexion
		*Enophrys bison**	Pre- to postflexion
		*Leptocottus armatus**	Pre- to posflexion
		*Parophrys vetulus**	Preflexion (few), postflexion
		*Cottus asper**(?)	Pre- to postflexion
Bay only	Rare	*Apodichthys flavidus**(?)	Pre- to postflexion
	Common	*Gobiesox maeandricus**	Pre- to postflexion
		*Ascelichthys rhodorus**	Preflexion
	Abundant	*Lepidogobius lepidus**	Preflexion to ?

the abundance of surface-captured early larvae, but weak for numbers of deep-captured late larvae (Figure 1). Boehlert and Mundy (1987) suggested that early larvae were moving inshore along the entire coast during periods of onshore transport. Transforming larvae of English sole are present in the neuston and depend upon surface Ekman transport to arrive at the nearshore zone; sampling with large neuston nets has shown relatively high densities of transforming larvae of this species in the upper meter during months of peak recruitment (Shenker 1985). In contrast, late larvae enter the estuary along the bottom; they apparently recruit first to nearshore habitats, then migrate to the estuary mouth (Krygier and Pearcy 1986; Boehlert and Mundy 1987). The mean current patterns on the west coast may have resulted in the evolution of reproductive patterns such that most fish species spawn in the winter and early spring months when onshore surface transport dominates (Parrish et al. 1981). Deviations from the mean pattern of surface water transport may result in poor year-class strengths for species such as the Pacific hake *Merluccius productus* (Bailey 1981).

Several other mechanisms have also been proposed for movement to the nearshore zone, including population maintenance in eddies (Sale 1970). Eddy mechanisms have typically been used to explain the maintenance of populations associated with islands (Boden 1952; Emery 1972), but coastal studies off California suggest that eddy mechanisms might be important there as well (Hewitt 1981; Owen 1981). Population maintenance in the nearshore zone in an upwelling area may also be accomplished by use of countercurrent systems, whereby drift is modulated by changes in vertical distribution (Peterson et al. 1979; Wroblewski 1982; Figure 2). Such a mechanism, termed "larval navigation" by Crisp (1974), could maintain the nearshore ichthyoplankton assemblage noted off Oregon. Finally,

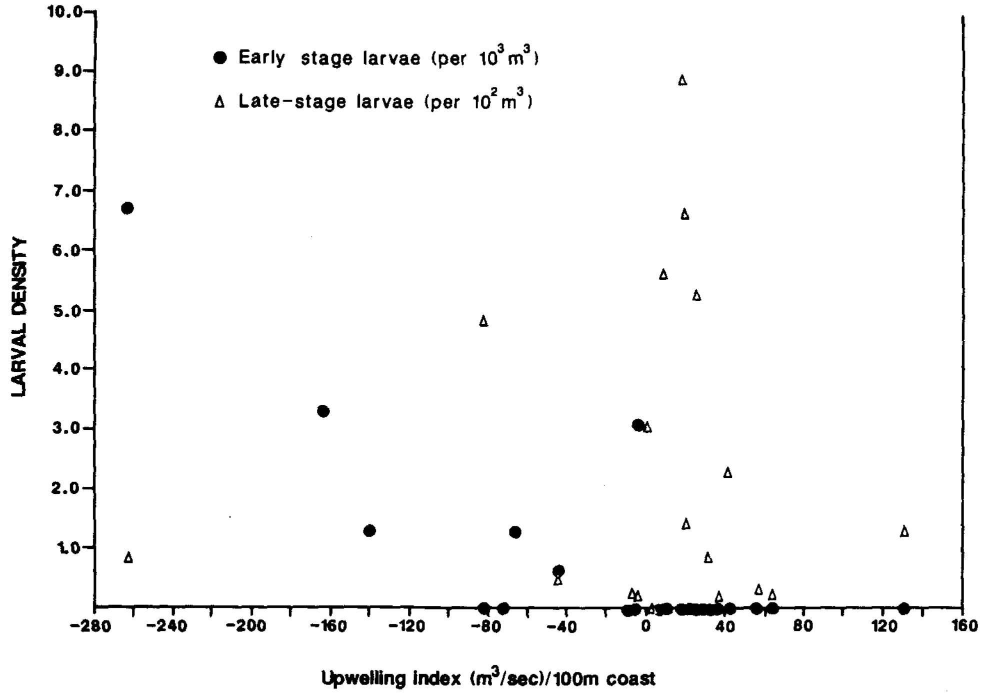

FIGURE 1.—Density of transforming larvae of English sole recruiting to Yaquina Bay, Oregon, as a function of the upwelling index. Early-stage larvae were taken by shallow nets; late-stage larvae were caught in nets set near the bottom, where these larvae are in higher abundance. Early larvae are abundant only during those times when the upwelling index is negative, suggesting onshore Ekman transport.

actual inshore movement may be modulated by accumulation in surface slicks, which in turn may be associated with internal waves (Shanks 1983, 1985; Kingsford and Choate 1986). Norris (1963) suggested a behavioral mechanism of orientation to these slicks; avoidance of the lower temperature at internal wave fronts by young opaleyes *Girella nigricans* would facilitate shoreward movement.

Estuarine Recruitment

Once larvae have recruited to the nearshore environment, a new set of physical factors influence their accumulation at inlets or estuarine mouths and their movements upstream into the estuary. Alongshore drift must play a key role in the movement of larvae to areas under estuarine influence. This influence may be more important on the west coast of North America, where only 10–20% of the coast is estuarine, than along the Atlantic and Gulf of Mexico coasts, which are 80% estuarine (Emery 1967). Krygier and Pearcy (1986) observed increases in the density of larval English sole in a nearshore nursery area distant from any estuarine influence. As densities at that location decreased, however, densities in Yaquina Bay, some 10 km to the south, increased, demonstrating a linkage between the nearshore and estuarine nursery areas. A southern alongshore drift may have brought the larvae near the estuarine mouth. The transition from northward to southward alongshore drift off Oregon typically occurs during March (Huyer et al. 1975), a period when the metamorphosing larvae enter Yaquina Bay (Krygier and Pearcy 1986; Boehlert and Mundy 1987).

Several physical factors near inlets or estuaries may serve as "point source" stimuli that could elicit short-term behavioral responses by larvae. Tidal flux may ultimately lead to accumulation, but tidal flux is a complex of related factors that cannot be isolated in field studies. This complex includes current speed, salinity (as affected by both river discharge and magnitude of tidal mixing and exchange), temperature, olfactory cues, turbidity, bottom composition (grain size), and lunar

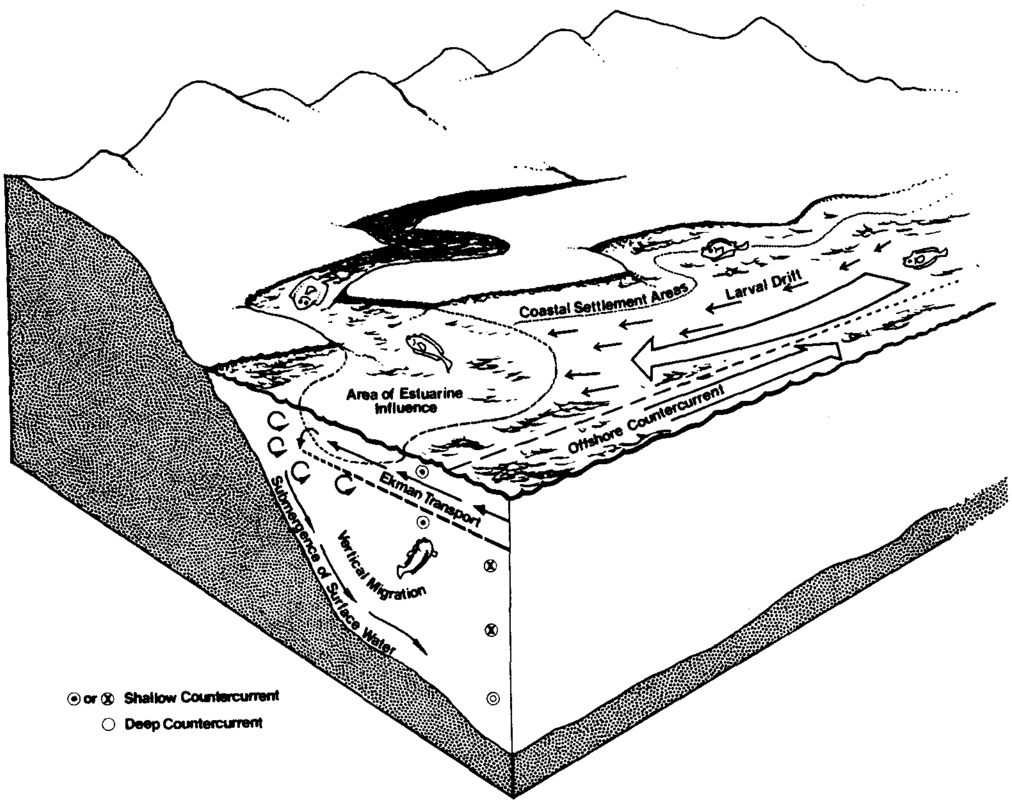

FIGURE 2.—Diagramatic representation of movements of larval fishes in the Oregon upwelling zone. Pelagic larvae may control onshore–offshore transport by their vertical movements, using surface Ekman transport to move shoreward (this condition pertains during the winter season off the Oregon coast). After larvae move near shore and settle, alongshore transport may result in movement to areas under estuarine influence.

phase. Individually and in concert, each factor may play a role in altering larval behavior patterns that facilitate recruitment. The complexity was pointed out by Hoar (1953), who suggested that "more rapid progress might be made if migrations which are not complicated by changes in osmotic medium are studied."

Many authors, including those cited previously, have monitored both recruitment to and maintenance in estuaries for a variety of taxa; results of these studies often are complex. Weinstein et al. (1980), who conducted one of the most detailed sampling studies, monitored movement of some commercially important species in an inlet in North Carolina. Catches of flounder *Paralichthys* spp. were greater on flood tides, particularly at night, which led the authors to suggest that the flounder postlarvae moved to the bottom during ebb tides. At night flood tides, flounders and spot *Leiostomus xanthurus* occurred high in the water column. Weinstein et al. (1980) suggested that this mechanism transported these two taxa to the tidal flats and creeks, which they used as nursery areas (Shenker and Dean 1979; Weinstein 1979, 1983). In contrast, postlarvae of Atlantic croaker *Micropogonias undulatus*, which use the head of the estuary, remained deeper in the water column, even at night. The model devised by Weinstein et al. (1980) may be used to explain both recruitment to and maintenance in estuaries (Figure 3); their results clearly show that species-specific behavioral responses to physical factors may result in different distributions within the estuary.

A suite of physical factors may serve as cues for such behavior. Several authors have investigated the relationship of animal distribution in the field to salinity and also the behavior of fish in laboratory tanks as a function of salinity. Many studies

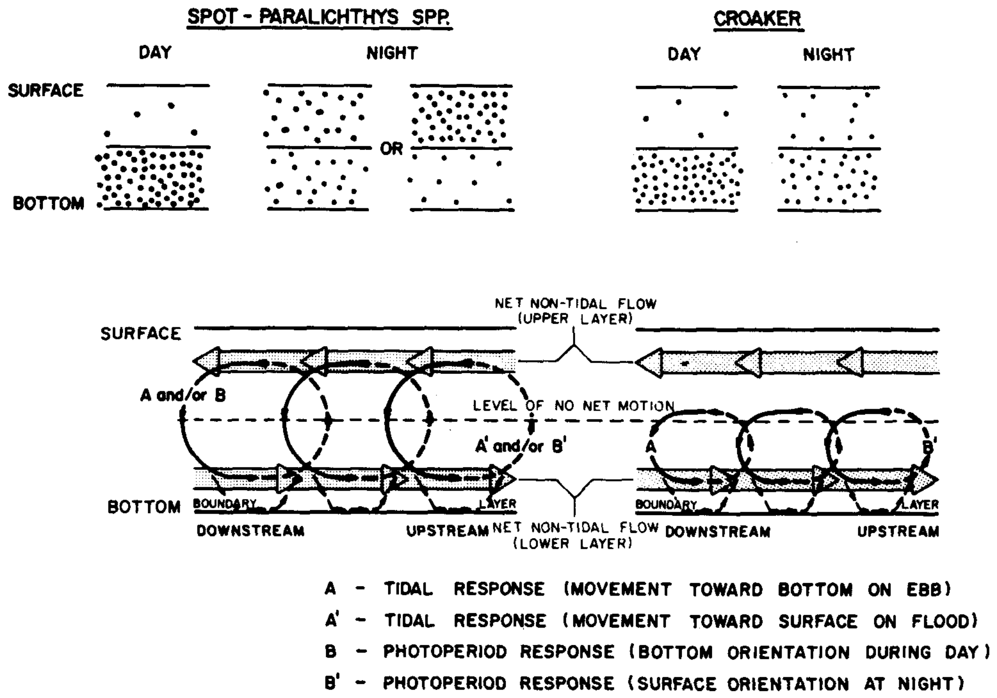

FIGURE 3.—A model of movements with the tide for three taxa of postlarval fishes in a North Carolina estuary, showing different strategies of tidal-stream transport. Spot and flounders use shallow tidal areas, whereas Atlantic croakers move to the upper reaches of the estuary, presumably by remaining deep in the water column at all times. (From Weinstein et al. 1980.)

have been based upon the classic work of Creutzberg (1961), who studied the immigration of European eel elvers *Anguilla anguilla* to tidal areas from the open sea. Field sampling demonstrated that the elvers swam actively in the water column on flood tides, but they were either near bottom or clinging to the bottom during ebb tides; this behavior pattern resulted in inshore movement. Creutzberg investigated the behavioral responses to increasing and decreasing salinity, but with "disappointing" results. More recent studies, particularly those with crustaceans, show clear responses to changes in salinity. Postlarval penaeid shrimp *Penaeus duorarum* move into estuarine nursery areas, whereas juveniles move out. Direct salinity changes, rather than some other factor, caused changes in behavior that resulted in the appropriate movements. Decreasing salinity caused benthic orientation by postlarvae and negative rheotaxis by juveniles; increasing salinity resulted in swimming behavior by the postlarvae but positive rheotaxis by the juveniles (Hughes 1969). The importance of salinity in determining the use of estuarine nursery areas by young shrimp is dramatically demonstrated by the strong correlation of offshore commercial shrimp catch with rainfall in the preceding year. Years with low rainfall have low salinity change near the estuaries and recruitment of postlarvae to estuaries is less successful. Salinity was also suggested as the controlling factor for emigration of the swimming crab *Macropipus holsatus* from estuarine areas (Venema and Creutzberg 1973); as with the juvenile shrimp, the crabs swim during decreasing salinity and settle to the bottom during times of increasing salinity, resulting in seaward movement. Physical variables are often highly intercorrelated, however, and speculations of causal relationships in such cases may be spurious. In our work with English sole, for example, there was a strong negative correlation between bottom salinity at the start of a flood tide and density of larvae recruiting to an estuary (Boehlert and Mundy 1987). Bottom salinity was highly correlated with other physical factors, however, including freshwater input, sea level, surface salinity, surface temperature, and other factors that may be related to recruitment. When larvae migrate onto nonestuarine tidal flats, they may encounter only very slight salinity differences, as in Elkhorn Slough, California (Yoklavich 1982), in the Gulf of Carpenteria, Australia (Staples 1980), or in some tropical areas (Pfeiler 1984). In the tropics, increased salinity caused by evaporation in hypersaline lagoons may allow salinity gradients to develop, but the salinity change is opposite that in estuarine systems. One must thus use caution in interpreting cause and effect in relationships between recruitment and single physical factors.

Temperature gradients between estuarine and offshore waters may be strong in temperate regions, particularly in winter months. Temperature is a candidate physical orientation factor for larvae because fish show temperature tolerances and preferences (Brett 1970). The majority of studies of temperature and migration, however, describe temperature-initiated migration out of an area. Hoar (1951), for example, showed that increasing temperature causes a change from positive to negative rheotaxis by young salmonids *Oncorhynchus* spp., facilitating downstream migration. Olla et al. (1980) showed that the tautog *Tautoga onitis* migrates to deeper water as temperature increases. Animals moving into estuaries might be seeking a preferred temperature, but more research is needed before any role of temperature in recruitment can be understood.

Other cues associated with water chemistry may play important orientation roles. Creutzberg's "disappointing" results with European eel elvers occurred when he altered salinity with tap water and observed no response, but when he diluted seawater with natural inland waters the elvers showed swimming behavior during increasing salinity and benthic orientation during decreasing salinity. Creutzberg (1961) suggested that some "attractive substance" in inland waters was the important factor in the immigration, rather than salinity alone. These results were later confirmed by Miles (1968) with elvers of the American eel *Anguilla rostrata*. He observed that some biodegradable component of either dissolved or particulate organic matter played a role. Thus some unknown "inland water odor," sensed through olfaction and similar to home-stream odors detected by adult salmonids (Hasler et al. 1978), may be involved. An alternative, but related, "odor" hypothesis is that a species- or population-specific pheromone may be involved (Nordeng 1977), but little evidence exists for this hypothesis.

Another olfactory cue is food odor, which may trigger activity if predatory larvae are unsatiated. Research on the movements of larval plaice *Pleuronectes platessa* in tidal areas showed that larvae were three times as abundant in the water column on flood than on ebb tides, resulting in net inshore transport (Creutzberg et al. 1978). Preliminary experimental data, however, suggested a mechanism of immigration different from that of other species studied. In the laboratory, neither salinity nor nursery "odors" stimulated behavior appropriate for transport, but starved animals exhibited greater swimming activity in the water column than fed animals. Although Creutzberg et al. (1978) proposed that tidal areas act as "traps" due to the abundance of food (as compared to offshore areas), they could not explain the stimulus for settlement. Gradients of food abundance may play a role in accumulation of young fish; Tanaka (1985) suggested that a gradient of copepod abundance, increasing from offshore to inshore, could lead immigrating red sea bream *Pagrus major* to inshore areas where the preferred prey, gammaridean amphipods, are present. Larval Atlantic herring *Clupea harengus harengus* may show vertical distributions within estuaries that are adaptive for population maintenance, but Fortier and Leggett (1983) suggested that these movements are simply a behavioral response to vertical movements of their prey organisms.

A variety of other candidate physical factors exist near entrances to estuaries that may elicit behavior appropriate for recruitment. Currents, a dominant feature of tidal flux, may be used, but only by fishes able to orient to a surface. Rheotaxis by young salmonids, for example, is lost in darkness, resulting in downstream movements (Hoar 1958). Transforming plaice, on the other hand, show different rheotactic responses depending upon their distance from a solid surface; within 3 cm of the surface, they are able to show normal rheotaxis even in darkness, but at greater distances they lose the ability to orient (Arnold 1969).

The use of electric or magnetic fields for orientation by fish larvae has not yet been demonstrated, but the elvers of American eels can detect relatively weak electric fields (McCleave and Power 1978). The thresholds for detection may be such that the relatively strong water currents (which cause electric fields) in regions of high tidal flux could be used for orientation. If this were the case, there would be no need for visual or tactile contact with the bottom, as discussed above with respect to rheotaxis.

Turbulence, turbidity, and light may interact to affect distributions. Fore and Baxter (1972) suggested that larval Atlantic menhaden seek less turbulent water and thereby accumulate in shallows and tidal creeks. In contrast, Blaber and Blaber (1980) observed the highest densities of juvenile fishes in the most turbid reaches of estuaries; negative phototropism may be involved in accumulation in such areas. Residence in turbid areas may result in decreased predation (Moore and Moore 1976; Gardner 1981). Some larvae, such as those of Pacific herring *Clupea harengus pallasi,* may indeed be adapted for feeding and survival in turbid estuaries (Boehlert and Morgan 1985). Rijnsdorp et al. (1985) suggested another relationship with turbulence; they observed a high correlation of suspended matter with the abundance of immigrating plaice larvae, suggesting that larvae may be swept up by stronger tides along with suspended materials. Flood tides at their study sites were typically stronger than the ebb tides, so their observations suggest that passive transport alone, with no behavioral change, could be important for immigration. Working with the young larvae of Atlantic herring, however, Fortier and Leggett (1983) noted no overall vertical dispersion during times of greatest vertical mixing of an estuary, contrary to the expectation that larvae would be passively mixed by turbulence (Fortier and Leggett 1982).

Lunar phase may affect transport of larvae into estuaries, but the mechanism is unknown. From a long-term study, Williams and Deubler (1968) suggested that lunar phase affects the timing of entry into estuaries for *Paralichthys* postlarvae and also for postlarval penaeid shrimps *Penaeus duorarum;* both groups were captured in greater numbers near the times of new moons than of full moons. This was later confirmed for penaeid shrimps by Roessler and Rehrer (1971). Similarly, catches of *Anguilla* elvers may show lunar periodicities (Jellyman 1979; Tzeng 1985). Tzeng (1985) obtained peak catches of riverine elvers at both new and full moons, correlated with spring tides. In coastal waters, however, peak catches occurred only during the new moon, suggesting that light inhibited activity there (Tzeng 1985). In all these studies, net avoidance is a confounding factor that may decrease catches during full moon. We observed no lunar periodicity in the immigration of larval English soles to Yaquina Bay, Oregon (Boehlert and Mundy 1987). Lunar phase is also coupled to changing tidal magnitude and, therefore, to salinity and temperature changes, current speed, and turbulence. Field or laboratory studies designed specifically to test hypotheses about the interrelationships among physical factors affecting immigration rates would be necessary to determine the roles of these physical factors.

Behavioral Responses to Estuarine Stimuli

The ability of organisms to orient to environmental stimuli underlies their movement to and retention in habitats that are optimal for survival. Aquatic organisms that inhabit different environments during ontogenetic development must respond to changing stimuli to orient to each new habitat. Recruitment to estuaries, we believe, is a behaviorally mediated rather than passive migration. To investigate migration, Hoar (1953) suggested that research " . . . should start with the behavior patterns of the fish; it should involve an analysis of the internal physiological states responsible for this restless appetitive behavior, and eventually, an understanding of the way in which this activity is guided and directed by the variables in the external environment." Behavior has generally been inferred from distribution in the field (changes in abundance), and correlation or statistical approaches have been used to relate results to physical variables. The appetitive behaviors necessary for recruitment may begin as either random movements (kineses) or directed movements (taxes). Organisms may accumulate during kinesis by changing rates of activity or rates of turning (Hunter and Thomas 1974) and during taxis by slowing movement when they reach the source of a directional stimulus. There are relatively few physical factors with vector properties; therefore, directed movements may be limited to phototaxis, geotaxis, and rheotaxis in response to light direction, gravity, and currents, respectively (Crisp 1974). Each of these factors might guide estuarine immigration, but they must be modulated by scalar factors such as salinity, temperature, turbidity, and olfactory cues; sequential sampling of a scalar factor through time or space may allow development of a directional sense through a learned response. These more advanced behavioral sequences, however, may be beyond the physical and sensory capability of larval or juvenile fishes, because current speeds in tidal inlets may prevent young fishes from controlling their horizontal position.

Tidal-stream transport is commonly cited as an example of vertical movement affecting horizontal displacement (Tsuruta 1978; Weinstein et al.

1980). Generally, the control of larval vertical distribution may arise either through taxis or kinesis. Fish larvae are frequently concentrated near thermoclines (Ahlstrom 1959; Loeb 1979), and kineses may explain accumulation over time within specific thermal regimes. Kinetic motion may be the most efficient way for larvae to find food under some circumstances (Hunter and Thomas 1974). Random kinetic motions cannot accomplish directed vertical movements, which must, therefore, be associated with a taxis or (as suggested by Fortier and Leggett 1983) with feeding excursions. No single mechanism has yet emerged as a general control of vertical placement for tidal-stream transport. Phototaxis of fish larvae has been documented extensively in the field and laboratory (Ahlstrom 1959; Blaxter and Staines 1970; Blaxter 1974; Hunter and Sanchez 1976; Kendall and Naplin 1981; Yamashita et al. 1985), but it typically operates on diel cycles. Reaction to both direction and intensity of light may explain the presence of immigrating larvae in night rather than day flood tides (Weinstein et al. 1980; Boehlert and Mundy 1987), but it cannot provide the temporal cue for activity on flood and not ebb tides. Similarly, geotaxis cannot account for observed periodicities in activity by larvae.

Rheotaxis of fishes plays an important part in tidal-stream transport; the subject has been reviewed by Arnold (1974, 1981). Fish can apparently detect current speeds of 1–10 cm/s (Arnold 1981), which are within or below the range of tidal currents, and the lateral line system, which detects water movements, develops relatively early in fish larvae (Iwai 1967). Thus, young fish may use currents and rheotaxis for recruitment to an estuary. This use is constrained by the need for either visual or tactile contact (Arnold 1969), as described earlier. Tidally generated turbulent fields within estuaries, however, may provide tactile cues under certain conditions (McCleave and Kleckner 1982).

Development and Behavioral Ontogeny in Relation to Movements

The stage of development at which fishes are present in inlets or estuaries may in large part determine their ability to behaviorally alter their distribution. For species spawned within an estuary, early larvae may be advected out, particularly from intensively flushed estuaries (Rogers 1940; Johnson and Gonor 1982). For those species using the estuary for a nursery, development may continue in offshore waters; Pacific herring, for example, are abundant in estuaries at certain times of year (Pearcy and Myers 1974), but they are also found in the nearshore assemblage of ichthyoplankton (Richardson and Pearcy 1977; Table 1). Resident species may be temporarily exported only to return to the estuary at a later stage (Johnson and Gonor 1982). In general, species that recruit to estuaries from offshore do so at advanced developmental stages, usually near or after metamorphosis; this is true for several orders of fishes, including Anguilliformes (Creutzberg 1961), Elopiformes (Pfeiler 1984), Clupeiformes (Miller et al. 1984), Perciformes (Weinstein et al. 1980; Tanaka 1985), and Pleuronectiformes (Tsuruta 1978; Boehlert and Mundy 1987).

Important changes occur at metamorphosis in sensory systems, behavior, and morphology that affect immigration to estuaries. Metamorphosis entails full development of fins and associated structural calcification, which result in better swimming capabilities (Blaxter and Staines 1971). Fukuhara (1985), for example, noted an increase in swimming speed of red sea bream from 1 body length/s for larvae to 4 body lengths/s for metamorphosed juveniles. Greater swimming ability may decrease a larva's chance of being flushed from the estuary, even during times of high freshwater input (Rogers et al. 1984). Many species undergo rapid changes in color and morphology in association with the change from pelagic to benthic existence (Hubbs 1958; Hunter 1967; Kendall et al. 1984). Major changes in structure and function of the retina occur (Blaxter 1974; Boehlert 1978; Kawamura and Hara 1980), including development of rods in the retina (Blaxter 1974) that are necessary for vision in dim light. Flatfish larvae undergo great changes in behavior at the time of metamorphosis (Fluchter 1965; Finger 1976; Gibson et al. 1978); they become benthic, and their rheotactic behavior effectively ceases (Arnold 1969). Kawamura and Ishida (1985) gave a detailed account of the changes in sensory systems and behavior from hatching to 72 d posthatch for the flounder *Paralichthys olivaceus*. In particular, they noted development of retinal rods at 25 d, disappearance of positive phototaxis at 30 d, and nocturnal activity at 33 d posthatch. It is during this 9-d period that the transition from the pelagic to benthic habitat occurs. Pfeiler (1984) described changes during metamorphosis of bonefish *Albula* sp., which shrink 60–65% as they enter hypersaline lagoons.

Generalizations about the methods of immigration for different fishes are difficult. but we wish to distinguish between perciform, anguilliform, and pleuronectiform fishes. Tanaka (1985) suggested that tidal-stream transport, which is important to flatfish and eels (Creutzberg 1961; Tsuruta 1978; McCleave and Kleckner 1982), is of secondary importance to perciform juveniles, which have more advanced swimming abilities but, perhaps more importantly, no ability to settle on the bottom. As they near metamorphosis, larval plaice and flatfish generally spend increasing amounts of time near the bottom, often alternating pelagic and benthic behavior (Fluchter 1965; Blaxter and Staines 1971). Given the proper behavior patterns with respect to tidal movements, these larvae could immigrate inshore using tidal-stream transport during flood tides and settling on the bottom during ebb tides; the energetic savings of this mode of migration approach 90% for juvenile fish (Weihs 1978). Blaxter and Staines (1971) observed that when larval plaice metamorphosed, their movement rates dropped from about 70 to 4 cm/min, the time they spent actively swimming changed from 95 to 10%, and the volume of water they searched (for food) dropped from 2,500 to 50 mL/h. This is a clear distinction from the changes noted above for red sea bream, a perciform (Fukuhara 1985). Although perciform fish use tidal stream transport (Weinstein et al. 1980), the benefits may be relatively low due to their inability to settle out on the bottom.

Relatively little work has been done on the influence of habitat type on larval settlement. Certain species may be able to delay transformation until they encounter suitable juvenile habitat (Pearcy et al. 1977; Moser 1981); this has recently been demonstrated, based on daily growth increments, for a coral reef fish (Victor 1986). Marliave (1977) found significant substrate preferences by settling larvae in five of six benthic species tested. The preferences seemed to be for structural features of the substrate that gave tactile cues to the settling larvae. Metamorphosing flatfish alternate between pelagic swimming and benthic resting behavior (Fluchter 1965), a behavior that may aid settling larvae in locating preferred habitats.

Role of Endogenous Rhythms

Another behavioral consideration important in recruitment to estuarine nursery areas is endogenous activity rhythms. As already noted, many of the physical factors associated with tidal flux have clear temporal signals but lack directionality. Temporal cues, or "zeitgebers," exist for setting internal clocks for individuals in nearshore areas under the influence of an estuarine system. A wide variety of evidence supports the presence of endogenous rhythms in fishes (see Thorpe 1978), including studies of activity patterns (Gibson 1965), retinomotor movements (Olla and Marchoni 1968), photosensitivity (Davis 1962), and biochemical patterns (de Bras 1979). The actual timekeeping mechanism may be a chemical phenomenon mediated by the pineal gland (Binkley et al. 1978; Matty 1978).

Endogenous rhythms may be daily, tidal, or lunar in periodicity. They can be observed experimentally, in the absence of temporal stimuli, for varying periods before they revert to a free-running rhythm. They are synchronized by normal environmental cycles to the appropriate periodicity (Enright 1975). Within species, endogenous rhythms may change during ontogeny. Planktonic plaice larvae are most active near the surface at night, but the rhythmicity is a function of light, rather than of any endogenous rhythm, because it disappears in constant light or darkness (Gibson et al. 1978). After planktonic larvae undergo a short period of relatively little activity (Blaxter and Staines 1971) and settle, newly benthic larvae maintain diel activity peaks. Populations remaining offshore retain this diel pattern, but nearshore or estuarine populations exhibit marked tidal activity patterns that are often of an endogenous nature (Gibson 1978; Gibson et al. 1978). That these rhythms change with changing habitat suggests that they may play an important role in habitat selection.

Endogenous rhythms in general were reviewed by Enright (1975); tidal rhythms have been reviewed by Palmer (1973) and Gibson (1978). Tidal rhythms generally relate to activities important for foraging, respiration, and movement and to other activities affected by tidal cycles. Tidal rhythms have been demonstrated for many species of fishes (Gibson 1978). The entrainment of the circatidal rhythm must occur after young fish come under the influence of estuaries in nearshore waters. Appropriate zeitgebers for synchronizing circatidal rhythms include pressure (Gibson 1971) and turbulence (Enright 1965) and, possibly, inundation and temperature (Palmer 1973). Cyclic changes in salinity in estuarine areas could also act as a zeitgeber. It is important that rhythms are set by local conditions, because tides differ in magnitude and phase over the range of most species. Some species such as the English sole may use different cues in different areas, because some estuaries they occupy have freshwater inputs and others have nearly none (Yoklavich 1982; Boehlert and Mundy 1987). If such species develop endogenous rhythms as they immigrate to estuaries, it is likely that the suite of physical factors associated with tidal flux, rather than a single factor, may serve as the zeitgeber. This is supported by the lack of a conclusive experimental identification of the zeitgeber for a tidal rhythm. Also, laboratory-reared animals have circadian rhythms instead of the circatidal rhythms found in field-collected animals of the same species (Gibson et al. 1978; Cronin and Forward 1979, 1983).

Hughes (1972) demonstrated endogenous, circatidal rhythms of swimming by the shrimp *Penaeus duorarum* over 3 d under constant conditions; he suggested that the postlarval shrimp were pelagic, drifting with the current during flood tide but exhibiting benthic behavior during ebb, resulting in movement into and up the estuary, much in the way described for fish by Weinstein et al. (1980; Figure 3). The significance of such a circatidal rhythm is obvious; if a single cue such as salinity or odor is used as a stimulus for pelagic or benthic behavior, there is no mechanism for the animal to detect the end of flood tide (McCleave and Kleckner 1982). Because the drifting animal will remain in the same water mass until it mixes with ebbing water, considerable downstream transport may occur. Linking the behavioral pattern to a circatidal rhythm would allow the animal to settle from the water column at the end of flood tide in the absence of stimuli associated with water quality, resulting in more efficient migration. Such rhythms must play a key role in tidal stream transport.

Behavioral Model of Recruitment to Estuaries

In studies of fish recruitment to estuaries, researchers typically consider spatial and temporal patterns of distribution and correlate them with a wide range of physical variables to infer the behavioral responses by the immigrating fish (Tsuruta 1978; Boehlert and Mundy 1987). In the laboratory, however, effects of physical factors generally are considered in isolation (Creutzberg 1961), often with somewhat surprising or enigmatic results (Creutzberg et al. 1978). Problems may arise due to artifacts associated with the laboratory environment, as shown by different behaviors of laboratory-reared and field-captured animals (Gibson et al. 1978; Cronin and Forward 1979, 1983). In this section, we consider a conceptual model for the behavior of fish and their responses to physical variables or other stimuli as they affect recruitment to estuaries. Such a model may be useful in the development of testable hypotheses.

Certain field studies have suggested mechanisms of estuarine recruitment that are entirely passive and require no behavioral response on the part of the larvae (Rijnsdorp et al. 1985). The majority of information on fishes, however, suggests otherwise. Most movements can be classified as a form of tidal-stream transport, and thus behavioral considerations associated with migration are pertinent, but we frame our model in terms of the process of habitat selection. Sale (1969) considered habitat selection as a negative feedback mechanism; stimuli from the environment, monitored by sense organs, feed into a "selection mechanism" which then triggers "appetitive exploration." In fishes, appetitive exploration may take many forms, from simple activity to changes in vertical distribution to rheotaxis or phototaxis. As a kinetic movement, such searching behavior may ultimately result in accumulation in more favorable environments where random activity will be reduced (Hunter and Thomas 1974). Sale suggested that in an adequate or optimal environment, the intensity of feedback is relatively low, which may eliminate or reduce appetitive exploration. In an inadequate environment, the feedback intensity increases, resulting in a greater percentage of the animal's time being spent in searching behaviors. Sale (1969) provided support for this hypothesis for habitat selection by showing that young manini *Acanthurus triostegus* reduce their exploratory behavior in an appropriate environment. Because fishes change optimal habitats with growth, the stimuli important for the "selection mechanism" most likely change throughout ontogeny as habitat requirements change. This was observed by Norris (1963) in a study of the selection of thermal habitats by opaleyes.

In the context of an estuarine system, Sale's model is more applicable than are simple concepts of taxes or kineses. The suite of physical factors is complex and, during ontogeny, larvae must select among several habitats. Our conceptual model (Figure 4) is generalized to allow application to a variety of species. We consider four habitats sequentially occupied by migrants; the dominant physical process in the habitat, the stimuli inducing the fishes' behavior, and the dominant activity pattern of the fish all determine the transition from

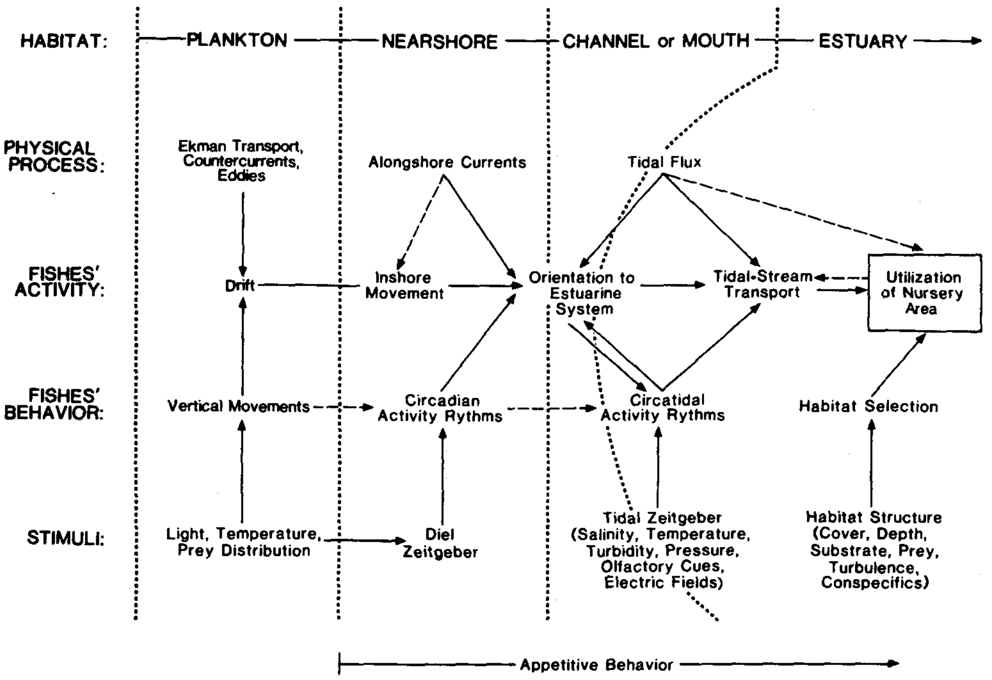

FIGURE 4.—A conceptual model for the role of stimuli and behavior in fish movement to estuarine nursery areas.

one habitat to the next. We first consider the offshore planktonic habitat, where the eggs and larvae are distributed. Here, the dominant physical factors are Ekman transport, countercurrents, and eddies (Parrish et al. 1981; Miller et al. 1984; Figure 2). Light, temperature, and prey distribution may be the key stimuli affecting vertical distribution, which may control the passive pattern of drift, both onshore–offshore and alongshore. This process may be one of critical importance to survival and one that may vary interannually, resulting in variations in year-class strength for both estuarine- and nonestuarine-dependent species (Nelson et al. 1977; Bailey 1981; Parrish et al. 1981).

Later larvae enter the phase of appetitive behavior as they begin searching for benthic habitat. A successful transition from the planktonic to the nearshore habitat involves "settlement," which may be taken literally in the case of a pleuronectiform but which may be referred to as "benthic orientation" for perciforms. In this initial settlement, substrate type and depth may be important factors (Marliave 1977). This is a major change usually involved with the process of metamorphosis. For species utilizing estuaries, the nearshore zone is a transitory habitat. Although we generally suggest that only late larvae recruit to the benthic nearshore habitat, more recent studies are documenting surprisingly large concentrations of various stages of fish larvae near bottom or rocky reefs (Brewer et al. 1981; Marliave 1986). Additional data may change our thinking about the process of recruitment to the nearshore zone. Later-stage larvae have increased powers of locomotion. At this stage, rhythmic activity may begin to play an important role in behavior and a circadian rhythm may develop (Gibson et al. 1978). Since the majority of fishes immigrate to estuaries at night (Pfeiler 1984; Tzeng 1985; Boehlert and Mundy 1987), it is probable that nocturnal activity is the rule; swimming activity, along with the movement induced by alongshore currents, may result in movement to the next transitory habitat, the channel or mouth of the estuary (the area of "estuarine influence" in Figure 2).

In Sale's (1969) hypothesis for habitat selection, the "intensity" of stimuli near the channel mouth would vary with a tidal periodicity. During ebb tides, settlement or bottom orientation might be induced by the factors associated with tidal flux (Figure 4), whereas the intensity of these stimuli would change during flood tides, as offshore water moves into the estuary. This condition would occur if a simple stimulus–response behavior exists. Such behavior patterns have been suggested for shrimp with salinity as the stimulus (Hughes 1969), for *Anguilla* elvers with "inland water odor" as the stimulus (Creutzberg 1961), and for plaice larvae with olfactory cues from prey as the stimulus (Creutzberg et al. 1978). Although such behavior would result in a form of tidal-stream transport, response to a single stimulus is a relatively simplistic mechanism and would not occur until a tidal change was well underway (McCleave and Kleckner 1982). Further, flow patterns around the mouths of estuaries are sufficiently complex to decrease the probability that a single factor changes consistently with a tidal periodicity (Ozsoy and Unluata 1982). Instead, we propose that a suite of stimuli associated with tidal flux acts as a zeitgeber to superimpose a circatidal rhythm upon the circadian rhythm which already may be present (O'Connor 1972; Gibson 1978). In this case, nocturnal swimming activity on flood tides and benthic orientation during other times could result in tidal-stream transport and movement up the estuary.

The process of estuarine recruitment may be a continuing one for some species that depend upon the process of habitat selection once inside the estuary (Figure 4). Weinstein et al. (1980) suggested that different vertical distribution patterns during tidal flux result in species-specific distributions within the estuary (Figure 3). The wide range of habitats present, and the new set of stimuli (vegetation, turbulence, prey distribution, substrate type) they provide, can lead to selection of shallow areas where flushing from the estuary is not a problem (Weinstein 1983; Rogers et al. 1984) or, conversely, to selection of areas near inlets where tidal-stream transport may be a continuing process necessary to maintain the fish within the estuary.

Sampling studies near the mouths of estuaries have provided a wealth of information on the movements of larval and juvenile fishes through inlets. Generally, these have led authors to generate hypothetical schemes of behavior involved in recruitment to and maintenance within estuaries. To date, laboratory studies (Creutzberg 1961; Miles 1968; Arnold 1969; Creutzberg et al. 1978; McCleave and Power 1978) on behavior of fishes relative to estuarine recruitment have tested some of the field-generated hypotheses on behavior, but they typically have used simplified designs that may not be meaningful to the field situation. More comprehensive studies on endogenous rhythms in fishes, including the array of zeitgebers as they relate to tidal-stream transport, are necessary; however, the behavioral complexity and activity patterns of fish larvae during transformation require that experimental facilities be larger than they have been so they can mimic natural environments.

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