Chapter 8
Diel and Tidal Movements by Fish and Decapods Linking Tropical Coastal Ecosystems

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Abstract Short-term movements of fishes and decapods can lead to regular changes in biomass, diversity, mortality, predation, and flux of energy between adjacent ecosystems. At low latitudes the day-night cycle is relatively stable and uniformly affects activity rhythms of marine organism at all longitudes. In contrast, tidal ranges and tidal types differ significantly between coasts and regions. On coasts with weak tides, twilight migrations connect adjacent habitats. On tidal coasts, migrations are tightly coupled to the interactive effect of the diel and tidal cycles which results in complex but predictable patterns of change within and between ecosystems. Diel and tidal migrations share several similarities (connection of resting and feeding sites, sequence of species and size groups, site fidelity, homing, constant pathways). The spring-neap tide cycle and its interaction with the diel cycle is a key factor influencing regular short-term variations on tidal coasts. The home range of a species on a macrotidal coast may be an order of magnitude greater than that of conspecifics from a microtidal coast, suggesting a need for larger marine parks on macrotidal coasts. Regional comparisons, e.g., between the Caribbean and the Indo-West Pacific, often disregard the significant tidal differences inherent to the ecosystems. It is suggested here that broad-scale comparisons must be redefined; regional comparisons should focus on geographical regions with similar tidal regimes, or on systems with different tidal regimes but with similar species communities.

Keywords Shallow-water fishes · Twilight migration · Lobsters · Shrimps · Portunid crabs

8.1 Introduction

The shallow waters of tropical coasts are home to unique ecosystems such as coral reefs and mangrove forests. Where coral reefs, mangrove forests, and seagrass beds co-occur, the ecosystems are usually connected with one another through the

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movements of organisms, nutrients, and other materials. In many tropical regions, coral reefs and seagrass beds form a mosaic of patches within a matrix of sandy sediments. Extensive mangrove forests grow within a complex network of sublittoral channels and intertidal creeks, mudflats, and sand banks. For some species, one habitat within a complex seascape setting is sufficient to complete its life cycle. For most other species, however, one habitat cannot satisfy the changing needs. Mobility is the solution to local deficiencies and the species move between different available habitats at different temporal and spatial scales. These movements can occur on a longer time scale such as on a seasonal basis or once during ontogeny (see Chapters 6, 7, 10), or on a shorter time scale according to the lunar, diel, or tidal cycle. When adjacent habitats are used on the short-term scale, the movements greatly affect the everyday life of an organism and likely influence growth and survival. In this chapter, the focus is on the short-term movements of fish and decapods in tropical shallow-water environments in relation to the diel and tidal cycles. It should be noted that all nektonic organisms (organisms living in the water column that can swim strongly enough to move counter to modest water currents) display movement, but not all migrate. For the purpose of this review, I refer to the general definition of migration as discussed by Dingle (1996): ‘Migratory behavior is persistent and straightened-out movement effected by the animal’s own locomotory exertions or by its active embarkation on a vehicle. It depends on some temporary inhibition of station-keeping responses, but promotes their eventual disinhibition and recurrence’. In the special case of this review, migratory movements connect adjacent habitat types or ecosystems, and involve a regular directional and temporal component.

A migration persists as an evolutionary stable strategy when the benefits exceed the costs. The ability to move enables species to optimize the use of resources in more than one ecosystem. A particular species exploits an ecosystem when benefits are high and avoids it when the benefits are low relative to other available ecosystems. The pay-off of a migration depends on the benefit provided by the present ecosystem, the cost of movement to another ecosystem, and by the expected conditions in an alternative ecosystem. For example, movement to a potentially profitable adjacent ecosystem would not pay off when the ecosystem is too far away, or when the risk of predation precludes its use at a given time of day.

Short-term migrations between adjacent ecosystems usually serve at least one of five functions (Gibson 1992, 1996, 1999, Gibson et al. 1998, Rountree and Able 1993): (1) feeding, (2) shelter or reducing the risk of predation, (3) avoidance of inter- and/or intraspecific competition, (4) reproduction, and (5) searching for a physiologically optimum environment.

Mobile organisms that shuttle between ecosystems influence each of the ecosystems used. Short-term migrations (i) change the species diversity and abundance counts in a given ecosystem (Thompson and Mapstone 2002), (ii) are a vector for the export of organic matter and nutrients from feeding to resting sites (Meyer et al. 1983, Meyer and Schultz 1985), (iii) regularly change the biomass of organisms in an ecosystem (e.g., Nagelkerken et al. 2000), (iv) shape patterns in herbivory and mortality in the feeding grounds (e.g., Ogden and Zieman 1977), and (v) shape the ecological value to the organisms of a given ecosystem. If a given ecosystem is out of reach for short-term migrants due to an unfavorable seascape configuration, the ecosystem cannot perform its potential values (Baelde 1990, Dorenbosch et al. 2007). The connectivity between shallow-water ecosystems caused by short-term migrations of fish and decapods has received increasing attention (e.g., Sheaves 2005), but with the major drawback that studies have been mainly conducted in the Caribbean where the influence of the tide is virtually absent. Surprisingly few studies on the topic come from Australia and the Indo-Pacific region and even less from African coasts.

Understanding the spatial and temporal dynamics caused by mobile organisms that use different habitat types at different times of day and at different tidal stages is crucial to sampling design, interpretation of ecological studies, and ecosystem management (Pittman and McAlpine 2003, Beck et al. 2001, Adams et al. 2006). Migrations can lead to faulty or incomplete population censuses or confounding effects in catch rates from a single ecosystem (e.g., Wolff et al. 1999). Optimized sampling strategies designed to measure long-term changes have to account for the short-term effects of migrations, e.g., considering the variation caused by the spring-neap tide cycle. The spatial and temporal patterns in short-term migrations determine the routine, everyday movements within the home range of mobile species and the connectivity between adjacent ecosystems. This information is required for population dynamics, spatial population models, and resource management (Cowen et al. 2006).

Fishes and most decapods are nektonic organisms. Many are commercially important, and as they are often caught together and interact ecologically (e.g., in predator-prey relationships), these species are addressed jointly in this chapter. For more information on the movements of their larvae see Sale (2006) for coral reef fishes, and Dall et al. (1990) for Penaeidae.

In this chapter an applied overview of the effects by which diel and tidal cycles influence the activity and use patterns of fish and decapods in the tropics will be given. The description of the distribution of tidal ranges and tidal types on tropical coasts highlights the diversity and regional differences in tidal regimes between coasts and regions. The review on the diel movements of fish is focused on examples from the Caribbean, the best studied and largest tropical area with negligible tides. The review of diel movements of decapods covers diel changes in activity and foraging ranges of lobsters, shrimps, and swimming crabs. The tidal movements of fish provides an overview on the variety of responses displayed by individuals, size groups, sexes, species, populations, and assemblages in response to the tide-time of day interactions. The section provides a comparison of the similarities and differences between diel and tidal migrations. The tidal movements of shrimps and swimming crabs highlight the interactive influence of the diel and tidal cycles on activity patterns. A regional comparison contributes to the debate on differences in connectivity between the Caribbean and the Indo-West Pacific. The final sections cover two aspects which have been largely overlooked in previous studies: the possibly greater home ranges of species in areas of greater tidal range, and the need to consider the influence of the tides when studying and comparing ecosystem functions and biodiversity patterns.

8.2 The Diel Cycle

The length of the diel cycle is 24 hrs, or the time it takes for the Earth to make one complete rotation around its axis. Due to the inclination of the Earth's axis by 23.5°, day length and solar irradiation differ with latitude and season. The diel cycle in the tropics differs from that in higher latitudes in two important aspects: (1) in lower latitudes, there is a relatively fixed cycle of approximately 12 hrs light and 12 hrs darkness year-round, whereas in temperate regions day length can vary between 16 hrs in summer and 8 hrs in winter, and (2) in the tropics the transition or twilight period at sunrise and sunset is relatively short (approx. 1 hr) whereas these periods can last for hours at higher latitudes. Consequently, in the tropics changes in illumination levels are highly consistent throughout the year and consequently, changes in the activity of most tropical organisms are well synchronized with the diel cycle. Four distinct diel periods can be distinguished that structure the activity patterns of most organisms exposed to light: sunrise, daytime, sunset, and night. Helfman (1993) classified the diel activity of fish families into diurnal, nocturnal, crepuscular (active at dusk and dawn), and two groups without clear activity periods. One notable example of the influence of the twilight period on fish behavior and distribution is the regular species changeover before and after the 'quiet period' in the clear water environment of coral reefs (Hobson 1972). However, even in the very turbid waters of mangrove estuaries, upsurges in the activity of fishes occur during twilight (Krumme and Saint-Paul 2003).

Sunlight is also reflected by the moon. The effect of moonlight on the activity of aquatic organisms depends on the lunar phase, cloud cover, water clarity, and water depth of an organism. Artificial light originating from fisheries and coastal construction, which brightly illuminates coastal areas for hours each night, may also be considered. With the exception of sea turtles, our understanding of the effects of light pollution on changes in the activity patterns of marine species is still in its infancy.

8.3 The Tides and Tidal Currents

This section does not present an exhaustive account of tides. The focus is on tidal characteristics which influence, or are in some way relevant to, the movement of nektonic organisms. General information on tides can be found in oceanographic textbooks (e.g., Dietrich 1980).

Tides are a complex natural phenomenon (e.g., Kvale 2006), which may be described as the periodic rise and fall of the sea surface level. A tidal current refers to the horizontal flow. Tides are mainly generated by gravitational forces of the moon, and to a smaller extent by the sun. Several factors such as the shape of the sea floor, local bathymetry, coastal morphology, the Coriolis effect, and changes in freshwater discharge, wind or air pressure act together to form a local tidal regime (Dietrich 1980). For nektonic organisms, tidal currents provide a mode of free transport. Tidal currents regularly reverse and can be used to selectively travel in a particular direction (selective tidal stream transport) or to commute between low and high tides, enabling an organism to move back and forth.

8.3.1 Short-term Patterns

A flood tide is defined as a rising of the water level (incoming tide); the ebb tide is the fall of the water level (outgoing tide). The point at which current speed and current direction are at zero and the tide turns from flood to ebb tide is termed slack high water. A tidal cycle lasts from one phase of the tide to the recurrence of the same phase. The tidal range is the difference in water level between low tide and high tide. Tides are of a semidiurnal, diurnal, or mixed type. (1) The semidiurnal tide is the most common tide (Fig. 8.1a) and is characterized by the biggest ranges and fastest current speeds. Two tidal cycles, each of 12 hrs 25 min duration, are observed on the coast each day, with small differences between successive high and low water levels. (2) Diurnal tides have only one tidal cycle per day (24 hrs 50 min) (Fig. 8.1b). (3) Mixed tides are predominantly diurnal (Fig. 8.1c) or semidiurnal (Fig. 8.1d). Mixed tides often display large differences in the heights of high or low water, or in both.

The fact that the lunar day period lasts 24 hrs and 50 min means that each tidal cycle is completed with a time delay in relation to the diel cycle (Fig. 8.1). Thus, in a sense each tidal cycle is a unique event and cannot be replicated. For example, if today slack high tide was at midday, then after six, twelve and fourteen days slack high tide will occur at 17:00, 22:00, and 23:40 hrs, respectively. The delay from tide to tide causes significant interactions between the tidal and diel cycles, with far-reaching consequences for the activity patterns of coastal organisms. The investigation of these complex interactions requires sophisticated sampling designs (see, e.g., Kleypas and Dean 1983, Krumme et al. 2004). However, on a few coasts the tidal cycle is in phase with the diel cycle and low and high waters occur at approximately the same time each day (e.g., Indonesia, South Pacific, and Adelaide/Australia; American Practical Navigator 2002).

8.3.2 Spring–Neap Tide Cycle

The tidal range changes following the lunar cycle. Usually there is a delay of one or two days between the lunar phase and the effect of the tide. At spring tides (at approximately full and new moon when the sun, moon, and earth are aligned), tidal

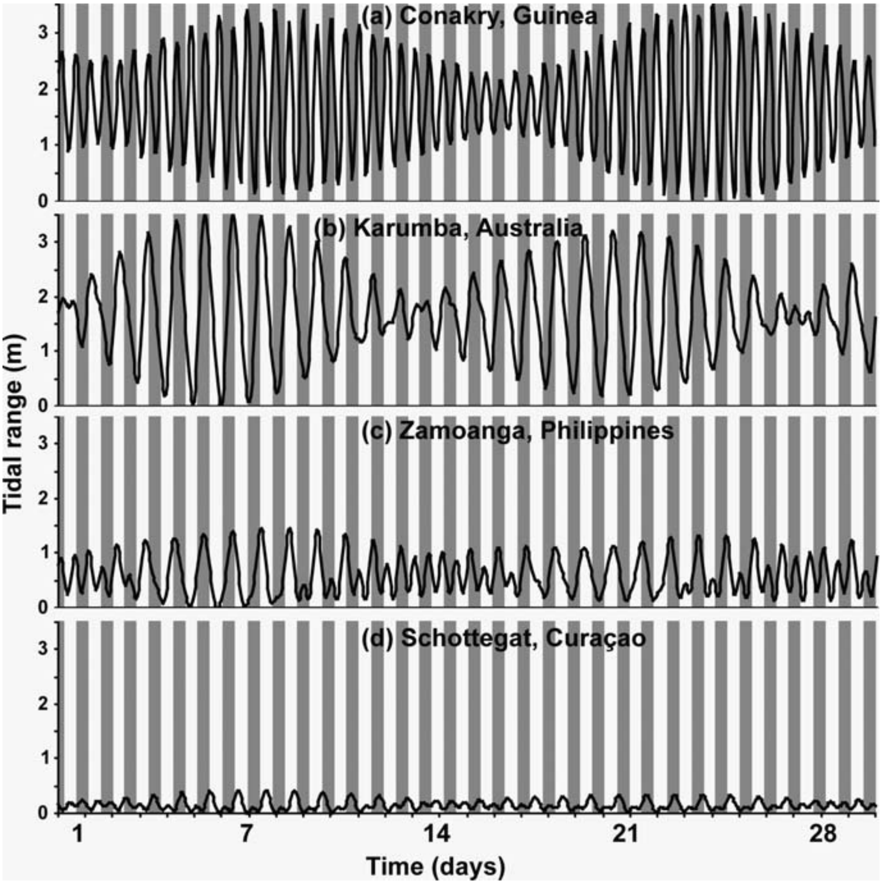

Fig. 8.1 Interaction of the diel and tidal cycles during one lunar cycle for a (**a**) semidiurnal tide (Conakry, Guinea; 13°43'W, 9°30'N), (**b**) diurnal tide (Karumba, Gulf of Carpentaria, Australia; 140°50'E, 17°30'S), (**c**) mixed-diurnal tide (Zamboanga, Mindanao, Philippines; 122°4'E, 6°54'N), and (**d**) mixed-semidiurnal tide (Schottegat, Curaçao; 68°56'W, 12°7'N). Shaded columns indicate night. Tide data from www.wxtide32.com

ranges and the current speeds reach a maximum. The slack high tide is extremely high and the slack low tide is extremely low. During neap tide (at the waxing and waning of the moon, when the earth and moon are perpendicular to each other) tidal ranges are significantly reduced and current speeds are much weaker (Kvale 2006).

There are, however, exceptions to these norms, for example on the south eastern Gulf of Carpentaria, Australia, the lunar phases are unrelated to the spring–neap tide cycle (Munro 1975). Comparative investigations of coasts with more unusual tidal characteristics would contribute to our overall understanding of tidal movement patterns of nektonic organisms.

8.3.3 Extreme Tides

Extreme spring tides cause large-scale changes on our coasts. Mobile coastal organisms may synchronize large-scale movements such as home range relocation or ontogenetic shifts to other ecosystems. They occur on a regular basis: (1) At about equinox (each March 21 and September 21) spring and neap tides are extremely strong and weak, respectively. (2) Every 7.5 orbits (or every 221 days) the moon comes closest to the earth (perigree), either at full or new moon. Then, particularly strong tidal forces result in strong perigrean tides. (3) The nodal tide caused by variations in the moon's declination results in extremely high tides approximately every 18.6 yrs. Thus, very strong tides occur on a fortnightly (regular spring tides), seasonal, annual, and decadal basis, providing means of transport for organisms throughout their development stages, for both short- and long-lived coastal species.

On coasts with weak tides, meteorological effects may sometimes exceed the tidal range. For instance, in shallow water annual tides are often wind-driven. This can lead either to exceptionally high or low tides. In the Red Sea, catastrophic seasonal low tides can expose the reef flats to the air for hours in the summer (Loya 1972, Sheppard et al. 1992; Fig. 8.2). In the Gulf of Mexico extreme high tide periods due to meteorological and climatic events lead to saltmarsh accessibility for nektonic organisms (e.g., Rozas 1995).

Fig. 8.2 Reef flat exposed due to extremely low seasonal tide in the coral reef of Eilat, Red Sea. Picture from Loya (1972), with kind permission from Springer Science + Business Media and Y Loya

8.3.4 Predicted and Observed tides

Tide tables are only predictions. The observed tide can deviate considerably from the predicted tide. Site-to-site differences can be significant, especially in mangrove or coral reef areas where the tidal currents are channelized (Wolanski et al. 1992, Wolanski 1994). Three examples highlight the need to understand the tide at a study site:

(1) The duration of flood and ebb tide may be unequal, e.g., due to local topography or intertidal vegetation. Not only the time but also the current speeds differ between flood and ebb because a fixed volume of water flows faster during a shorter period, and slower during a longer period. This results in either flood or ebb-dominated systems. Tidal asymmetries most likely are reflected in the timing of tidal movements and usage patterns of nektonic organisms. Intertidal land reclamation and mangrove loss can modify the flood-ebb tide asymmetry and hence, the use patterns of nektonic organisms.

(2) In theory, flood and ebb current speeds and the rate of rise and fall reach a maximum halfway between slack high and slack low water. Nektonic organisms may respond specifically to this time window of maximum currents because it provides the greatest potential for transport. It may further coincide with the period of greatest turbidity, i.e., lowest visibility, and hence decreased risk of predation when moving with the tide. However, current speeds and water level change may differ during flood and ebb tide. In addition, a distinct current peak is often difficult to identify, especially with weaker tides. A distinct maximum may be undetectable, or a peak may be earlier or later than halfway between low and high tide. In interconnected channel systems, momentary stops or current reversals may occur during weak flood tides, leading to two or possibly even three distinct current speed maxima.

(3) In estuaries and channel systems tides can be extremely complex. The tidal currents in channels are characterized by significant vertical and horizontal gradients that may vary with estuarine location and tidal stage. Ebb tide currents are usually greatest close to the surface in the centre of a channel whereas flood tide currents may be stronger at subsurface depths. Furthermore, the currents tend to turn earlier close to the shore than in the midchannel. In layered estuaries flood tides may begin between a few minutes to >1 hr earlier at the bottom.

8.3.5 Distribution of Tidal Types and Tidal Ranges on Tropical Coasts

Unlike the diel cycle which has a clear latitudinal gradient and appears the same at any given longitude, tides vary strongly with coastal region, both in type and range. Davies (1972) and Hayes (1975) classified the hydrographic regime of marine coasts into micro-, meso-, macrotidal using spring tide ranges of <2 m, 2–4 m, and >4 m, respectively. Others use slightly different subdivisions and the relevance of this classification scheme for the movements of nektonic organisms is still unclear.

Figures 8.3 and 8.4 illustrate the complex modern pattern of tidal types and ranges on tropical coasts. Semidiurnal tides are characteristic of the Atlantic coasts and many coastlines are meso- or macrotidal. The enclosed Caribbean is

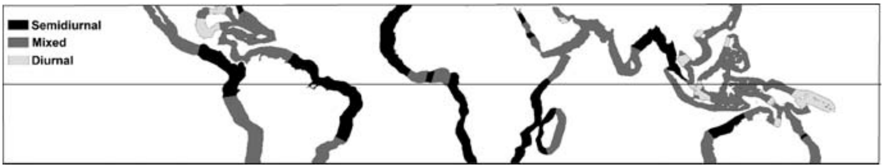

Fig. 8.3 Distribution of tidal types along the tropical coasts of the world. Mixed tides are not further separated into mixed diurnal and mixed semidiurnal tides. Adapted from Fig. 1.2 in 'Distribution of tidal types along the world's coast' in Davies (1972), Geographical Variation in Coastal Development, Oliver Boyd. Additional information used: Dietrich (1980), Eisma (1998), Admiralty Co-Tidal Atlas (2001), and www.wxtide32.com

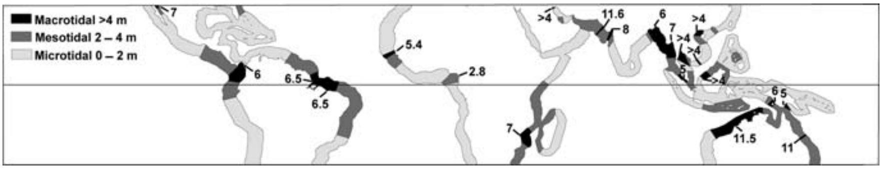

Fig. 8.4 Distribution of tidal ranges (in meters) along tropical coasts of the world. Adapted from Kelletat (1995). Additional information used: Dietrich (1980), Eisma (1998), Admiralty Co-Tidal Atlas (2001), and www.wxtide32.com

an exception in having mixed and diurnal tides with a tidal range of <1 m (e.g., in Curaçao, Fig. 8.1d).

In the Indian Ocean, tides are semidiurnal (e.g., East Africa, Bay of Bengal, Andaman Sea, Strait of Malacca, Northwest Australia) or mixed semidiurnal (e.g., Arabian Sea, Coromandel Coast, West Sumatra, South Java). The Red Sea is almost totally enclosed and tides are negligible, although in the Gulfs of Aqaba and Suez, spring tide ranges may reach 1–1.5 m (Sheppard et al. 1992).

The Pacific Ocean is dominated by mixed semidiurnal tides, for example the Great Barrier Reef with tidal ranges >3 m (Wolanski 1994). Semidiurnal and mixed semidiurnal tides characterize the East Pacific coast. Small tidal ranges are characteristic of islands in the open ocean. In the Indo-Malayan Archipelago the patterns are complex. Two regions can be differentiated: (1) The South China Sea and adjacent basins are dominated by mixed diurnal tides with tidal ranges from <1 m to >2 m (e.g., Zamboanga, Fig. 8.1c). However, within this area there are cells with distinct diurnal tides (e.g., western Gulf of Thailand, Gulf of Tonkin, north coast of Java), and cells with mixed semidiurnal tides (e.g., Singapore, Mekong Delta, Sarawak). (2) East of this area mixed semidiurnal tides dominate (e.g., east coast of the Philippines, Celebes Sea, northern New Guinea). Tidal ranges can be <1 m (Sulawesi), or exceed 2 m (east Indonesian islands, East Kalimantan). Again, within this area there is a diurnal cell at the southeast coast of West Papua.

In conclusion, tides are a common and regular natural disturbance of many tropical coastlines, except for the Caribbean, the Red Sea, a few cells in the West Pacific (e.g., the Java Sea), and many oceanic islands. The triangle of marine biodiversity between Indonesia, the Philippines, and Papua New Guinea coincides with the greatest diversity of tidal types and tidal ranges. The overall tidal ranges of the Indo-West Pacific are not exceptionally high, but undoubtedly are higher than the microtidal coasts of the Caribbean.

If we imagine the global distribution of mangroves, coral reefs, and seagrass beds (not covered here, but refer to Spalding et al. 1997, Spalding et al. 2001, Larkum et al. 2006) and superimpose it in the minds' eye on the global distribution of tidal ranges (Fig. 8.4), it is apparent that the coexistence of the troika mangrove-seagrass-coral reef is restricted to coasts with weak or intermediate tidal ranges and minor freshwater input. In contrast, the world's largest contiguous mangrove stands (e.g., the Sundarbans, the coasts north and south of the Amazon mouth, South Papua, and West Sumatra) grow on coastal plains where large rivers enter the sea and where tidal ranges are large. Due to coastal estuarization and high sediment loads in these areas, coral reefs and seagrass beds are excluded. Each ecosystem can thrive in the absence of the others, but where environmental conditions facilitate their spatial overlap, biodiversity and productivity can be significantly enhanced (Nagelkerken et al. 2002, Mumby et al. 2004, Dorenbosch et al. 2005).

8.4 Diel Movements of Fish

Most fish will alter their activity and patterns of movements following the day-night cycle. Diel movements of tropical coastal fish are most adequately studied where the influence of the tides is negligible. In the absence of tidal currents, distances between sites have to be covered by active movements. Hence, the benefits of moving (e.g., finding a rich food patch) have to outweigh not only the potential costs that incur also on tidal coasts (e.g., increased risk of predation) but also the cost of increased energy expenditure.

Daily twilight migrations are common among fishes of heterogeneous tropical marine seascapes (Table 8.1). Often these migrations connect one micro-habitat or habitat type that provides shelter with another that provides food. Diurnal reef-associated families such as Acanthuridae, Chaetodontidae, Labridae, Pomacentridae, and Scaridae move from their daytime foraging sites to nighttime shelter in crevices and cavities of rocks and corals, in seagrass or sediment. Nocturnal families such as Apogonidae, Haemulidae, Lutjanidae, Holocentridae, Pempheridae, and Sciaenidae shelter in or near complex structured resting sites through the day and migrate to adjacent feeding grounds at night (e.g., Hobson 1965, 1968, 1972, 1974, Starck and Davis 1966, Randall 1967, Collette and Talbot 1972).

8.4.1 Haemulidae

Certainly the best documented diel movement of fish is the twilight migration of grunts (Haemulidae/Pomadasyidae) between daytime resting sites on patch reefs and nightly feeding sites in adjacent seagrass beds (Figs. 8.5, 8.6). Grunts are

Table 8.1 Fish families and species that display regular diel movements between tropical coastal shallow-water habitats. Underlined habitats indicate the time of day when feeding occurs. Foraging range: distance between resting and feeding sites. Superscript numbers refer to the respective literature reference

		Residence at			
Fish family	Species	Day	Night	Foraging range	Region
Carcharhinidae	*Carcharhinus leucas*[1]	Offshore	Reef	–	Caribbean (Florida)
Acanthuridae	*Prionurus punctatus*[2]	Offshore rocks	Reef	–	Gulf of California
Acanthuridae	*Naso hexacanthus*[2]	Offshore	Reef	–	Hawaii
Anomalopidae	*Photoblepharon palpebratum*[3]	Reef	Away from reef	–	Red Sea
Apogonidae[9, 10, 11, 12, 13, 14]	*Apogon cyanosoma*[4] *Apogon doerderleini*[4] *Apogon exostigma*[4]	Reef	Above sand	–	Great Barrier Reef
Apogonidae	*Apogon fuscus*[5]	Reef	Seagrass	–	Gulf of Thailand
Apogonidae	*Apogon aureus*[6] *Apogon cyanosoma*[6]	Reef	Seagrass	–	Negros Oriental, Philippines
Apogonidae	*Apogon hartzfeldii*[7] *Apogon hoevenii*[7] *Sphaeramia orbicularis*[7]	Reef	Seagrass	–	Sulawesi, Indonesia
Apogonidae	*Apogon affinis*[8] *Apogon quadrisquamatus*[8]	Reef	Sand	–	Caribbean (St. Croix)
Apogonidae	*Apogon aurolineatus*[1, 15] *Apogon binotatus*[1, 15] *Phaeoptyx conklini*[1, 15]	Reef	Seagrass, midwater	–	Caribbean (Florida, St. Croix)
Atherinidae[14]	*Hypoatherina harringtonensis*[1, 15]	Reef	Seagrass, beyond the reef	<800 m[1]	Caribbean (Florida, St. Croix)

Table 8.1 (continued)

Fish family	Species	Residence at Day	 Night	Foraging range	Region
Atherinidae	*Pranesus insularum*[16]	Reef, schooling in shallow water or along the edge of channels	Off-reef, water surface	–	Hawaii
Atherinidae	*Pranesus pinguis*[17]	Reef	Offshore	1.2 km[18]	Marshall Islands
Aulostomidae	*Aulostomus maculatus*[13]	Reef	Seagrass	–	Caribbean (Panama)
Carangidae	*Caranx hippos*[19] *Caranx* spp.[12] *Scomberomorus* spp.[12]	Seagrass, reef, mangrove	Seagrass, reef	–	Caribbean (St. Croix)
Carangidae	*Selar crumenophthalmus*[20]	Close to shore	Sand	–	Gulf of California
Clupeidae[14]	*Harengula thrissina*[20]	Over rocks	Offshore sand	>500 m[18]	Gulf of California
Clupeidae	*Harengula humeralis*[1, 15] *Jenkinsia majua*[1, 15] *Jenkinsia lamprotaenia*[1, 15] *Sardinella anchovia*[1]	Reef, back-reef area	Seagrass, offshore	*J. majua* >800 m[1] *S. anchovia* >2 km[1]	Caribbean (Florida, St. Croix)
Clupeidae	*Jenkinsia lamprotaenia*[19, 21]	Mangrove	Windward side of the bay	–	Caribbean (Puerto Rico)
Clupeidae	Several species[1, 22]	Reef	Away from reef	–	Caribbean, Gulf of California
Congridae	*Conger cinereus*[6]	Reef	Seagrass	–	Negros Oriental, Philippines
Diodontidae	*Chilomycterus schoepfi*[1]	Reef	Seagrass	–	Caribbean (Florida)
Diodontidae	*Diodon holocanthus*[6]	Reef	Seagrass	–	Negros Oriental, Philippines
Engraulidae[14]	*Anchoa cayorum*[15] *Anchoa lamprotaenia*[15]	Reef	Seagrass	–	Caribbean (St. Croix)

Table 8.1 (continued)

Fish family	Species	Residence at Day	 Night	Foraging range	Region
Fistulariidae	*Fistularia tabacaria*[1, 13]	Reef	Seagrass, sand	–	Caribbean (Panama, Florida)
Gerreidae	*Eucinostomus* spp.[19] *Gerres cinereus*[19]	Mangrove	Sandflat, seagrass	–	Caribbean (Puerto Rico)
Haemulidae[1, 10, 13, 14, 20, 22, 25]	*Haemulon aurolineatum*[1, 15, 19] *Haemulon chrysargyreum*[1] *Haemulon flavolineatum*[19] *Haemulon parra*[19] *Haemulon plumierii*[8, 12, 19, 26] *Haemulon sciurus*[8, 15, 19]	Patch reef, mangrove, gorgonians[27]	Seagrass, sand	*H. aurolineatum* 800 m[1] *H. flavolineatum* 1.6 km[1] *H. sciurus* 400 m[1], 200–300 m[28], >1 km[12]	Caribbean (St. Croix)
Haemulidae	*Haemulon flavolineatum*[23]	Mangrove/Seagrass	Seagrass	–	Caribbean (Curaçao)
Haemulidae	No species names given[24]	Reef	Gorgonian site	–	Caribbean (St. Croix)
Haemulidae	*Anisotremus interruptus*[20]	Reef	Shallow water	–	Gulf of California
Haemulidae	*Haemulon sexfasciatum*[20] *Microlepidotus inornatus*[20] *Haemulon flavigutattum*[20] *Haemulon maculicauda*[20]	Reef, rock, inshore sandy bottom	Offshore sand	–	Gulf of California
Holocentridae[9, 10, 11, 12, 13]	*Holocentrus adscensionis*[15] *Sargocentron coruscum*[1, 8, 15] *Myripristis jacobus*[15] *Holocentrus marianus*[8] *Holocentrus rufus*[15] *Holocentrus vexillarius*[1, 15]	Reef	Seagrass, sand, rubble, rock	–	Caribbean (Florida, Panama, St. Croix)

Table 8.1 (continued)

		Residence at			
Fish family	Species	Day	Night	Foraging range	Region
Holocentridae	*Sargocentron rubrum*[5]	Reef	Seagrass	–	Gulf of Thailand
Holocentridae	*Myripristis argyromus*[2] *Myripristis berndti*[2]	Reef	Away from reef	–	Hawaii
Holocentridae	Species not identified[6]	Reef	Seagrass	–	Negros Oriental, Philippines
Holocentridae	*Holocentrus* sp.[29]	Reef	Dispersed at dawn	–	Great Barrier Reef
Labridae	*Halichoeres chloropterus*[5]	Seagrass	Reef	–	Gulf of Thailand
Lutjanidae[1, 2, 10, 12, 13, 22, 30]	*Lutjanus apodus*[1, 8, 19] *Lutjanus griseus*[1, 8] *Lutjanus synagris*[1, 8]	Reef, mangrove	Seagrass, sand, rubble, algal flats	*L. griseus* 1.6 km[1]	Caribbean
Lutjanidae	*Lutjanus argentiventris*[20]	Reef	Rocky areas near shore	–	Gulf of California
Mullidae[10, 12, 13, 18, 31]	*Mulloides flavolineatus*[32, 33]	Reef	Sand flat	600 m[33]	Hawaii
Mullidae	*Parupeneus porphyreus*[34]	Reef	Sand, coral rubble	–	Hawaii
Muraenidae[14]	Species not identified[6]	Reef	Seagrass	–	Negros Oriental, Philippines
Muraenidae[13, 35]	Unspecified	Reef	Seagrass/sand	–	Pacific Ocean, Caribbean (Panama)
Ophichtidae[14]	*Leiuranus semicinctus*[6] *Muraenichthys macropterus*[6]	Reef	Seagrass	–	Negros Oriental, Philippines
Pempheridae[14]	*Pempheris oualensis*[36]	Reef	To the sea	–	Red Sea
Pempheridae	*Pempheris schomburgkii*[1, 37]	Back-reef	Fore-reef	1 km[37]	Caribbean (Florida, St. Croix)
Plotosidae	*Plotosus lineatus*[6]	Reef	Seagrass	–	Negros Oriental, Philippines
Pomacentridae[2, 38, 39]	*Pomacentrus tripunctatus*[5]	Seagrass	Reef	–	Gulf of Thailand

Table 8.1 (continued)

		Residence at			
Fish family	Species	Day	Night	Foraging range	Region
Priacanthidae	*Priacanthus cruentatus*[2]	Reef	Away from reef	–	Hawaii
Scaridae[40]	*Sparisoma radians* (<15 cm)[12] *Scarus guacamaia* (>40 cm)[12]	Seagrass	Reef	–	Caribbean (St. Croix)
Sciaenidae[20]	*Pareques viola*	Reef	Sand	–	Gulf of California
Sciaenidae[35]	*Sciaena* spp.[18]	Reef	Seagrass/sand/rubble	–	Pacific Ocean
Sciaenidae	*Equetus acuminatus*[27]	Reef	Sand	–	Caribbean (Florida)
Scorpaenidae[41]	*Scorpaena grandicornis*[1]	Reef	Seagrass	–	Caribbean (Florida)
Serranidae[9, 13, 41]	*Epinephelus merra*[41]	Reef	Seagrass	–	Caribbean, Madagascar
Siganidae[42]	Unspecified	In or over coral heads	Away from coral heads	–	Unspecified
Sparidae	*Archosargus rhomboidalis*[19]	Mangrove	Sandflat, seagrass	–	Caribbean (Puerto Rico)
Sphyraenidae	*Sphyraena barracuda*[12]	Seagrass, reef	Seagrass, reef	–	Caribbean
Tetraodontidae	*Arothron stellatus*[6]	Reef	Seagrass	–	Negros Oriental, Philippines

References: [1]Starck and Davis 1966, [2]Hobson 1972, [3]Morin et al. 1975, [4]Marnane and Bellwood 2002, [5]Sudara et al. 1992, [6]Kochzius 1999, [7]Unsworth et al. 2007a, [8]Collette and Talbot 1972, [9]Randall 1963, [10]Randall 1967, [11]Vivien and Peyrot-Clausade 1974, [12]Ogden and Zieman 1977, [13]Weinstein and Heck 1979, [14]Helfman 1993, [15]Robblee and Zieman 1984, [16]Major 1977, [17]Hobson and Chess 1973, [18]Hobson 1973, [19]Rooker and Dennis 1991, [20]Hobson 1965, [21]Radakov and Silva 1974, [22]Hobson 1968, [23]Verweij et al. 2006, [24]Wolff et al. 1999, [25]Starck 1971, [26]Ogden and Ehrlich 1977, [27]Longley and Hildebrand 1941, [28]Quinn and Ogden 1984, [29]Domm and Domm 1973, [30]Hiatt and Strasburg 1960, [31]Jones and Chase 1975, [32]Hobson 1974, [33]Holland et al. 1993, [34]Meyer et al. 2000, [35]Hobson 1975, [36]Fishelson et al. 1971, [37]Gladfelter 1979, [38]Doherty 1983, [39]Foster 1987, [40]Ogden and Buckman 1973, [41]Harmelin-Vivien and Bouchon 1976, [42]Meyer et al. 1983 abundant Caribbean reef fish and their diel migrations mark a major link among shallow-water ecosystems. The most detailed studies originate from St. Croix, US Virgin Islands (Ogden and Ehrlich 1977, Ogden and Zieman 1977, McFarland et al. 1979, Quinn and Ogden 1984, Robblee and Zieman 1984, Beets et al. 2003), and

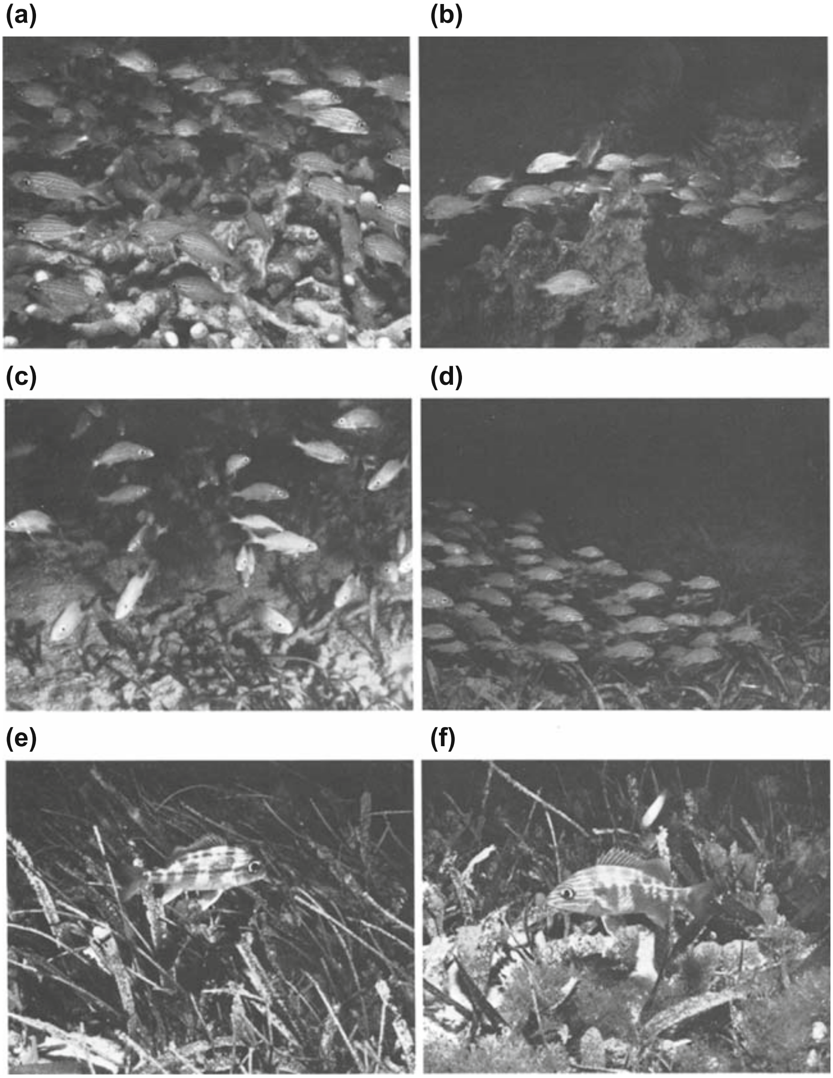

Fig. 8.5 Juvenile grunts in various phases of daily behavior in St. Croix, US Virgin Islands: (**a**) schooling on a patch reef during the day, (**b**) an 'assembly' at the staging area, (**c**) 'ambivalence' at the staging area, (**d**) evening migration of *H. flavolineatum* and *H. plumierii*, (**e**) solitary *H. flavolineatum* on grass bed at night, (**f**) solitary *H. plumierii* on grass bed at night. Pictures from McFarland et al. (1979), with kind permission from Springer Science + Business Media and JC Ogden

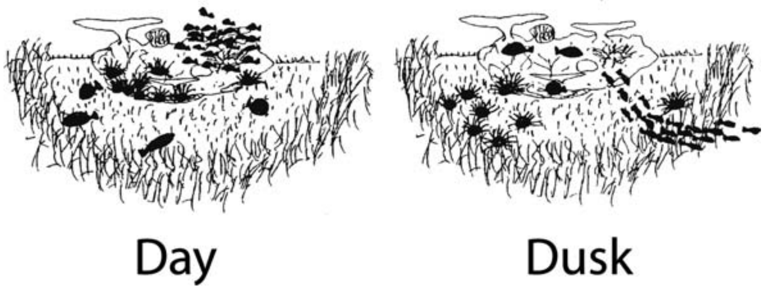

Fig. 8.6 Illustration of a Caribbean patch reef at daytime and at dusk. Picture from Ogden (1997), with kind permission from Springer Science + Business Media and JC Ogden

numerous studies have shown that the twilight migrations of juvenile grunts in St. Croix occur in heterogeneous seascapes throughout the Caribbean (e.g., Ogden and Ehrlich 1977, Panama: Weinstein and Heck 1979, Puerto Rico: Rooker and Dennis 1991, Tulevech and Recksiek 1994, Guadeloupe: Kopp et al. 2007, Curaçao: Nagelkerken et al. 2000, Belize: Burke 1995, Florida: Tulevech and Recksiek 1994).

These studies found that during the day mixed schools of juvenile grunts are inactive, resting on patch reefs surrounded by seagrass meadow. The dominant species were French grunts *Haemulon flavolineatum* and white grunts *H. plumierii*. Starck and Davis (1966) mention several other haemulid species involved in regular diel migrations to the reef adjacencies (Table 8.1). The start of the feeding migration off the reef at dusk is highly ritualized, comprising four behaviors (Fig. 8.5): (1) separate schools begin to stream along the reef surface (restlessness), (2) merge with other schools (assembly), and (3) finally concentrate on the reef edge (ambivalence) from where they (4) start the evening migration (departure) along fixed and constant corridors into the adjacent seagrass meadow (Ogden and Ehrlich 1977, Helfman et al. 1982). After up to 50 m linear movement away from the reef, small groups begin to disassociate from the main group and disperse in a dendritic pattern in the seagrass bed. Typically, the active migration takes the grunts to places 100–200 m away from the reef (Quinn and Ogden 1984), but sometimes >1 km (Ogden and Zieman 1977). The grunts forage solitarily for benthic invertebrates through the night. French grunts and bluestriped grunts (*H. sciurus*) seem to forage preferably in sandy areas, whereas white grunts forage on both sandy and grassy areas (Starck and Davis 1966, McFarland et al. 1979, Burke 1995), suggesting space and diet partitioning by the different species. Grunts display considerable flexibility in foraging ground use. They were observed foraging in seagrass, mangrove, sand, rubble, gorgonian habitat, and algal beds (Starck and Davis 1966, Ogden and Ehrlich 1977, Wolff et al. 1999, Nagelkerken et al. 2000). However, once established, nocturnal feeding territories are maintained over time (McFarland and Hillis 1982). Using acoustic telemetry, Beets et al. (2003) found high site fidelity for *H. sciurus* to nocturnal foraging sites in seagrass beds up to 767 m from diurnal resting sites.

It is not known if the grunts display a stereotyped behavior during their morning migration back to the reef. Usually the fish schools stream a few centimeters above the seagrass bed on the same pathway used during the evening migration to quickly arrive at their typical daytime resting position (McFarland et al. 1979). The proportion of the population of grunts that carry out twilight migrations is usually around 100%. Meyer et al. (1983) and Meyer and Schultz (1985) quantified the fertilizing effect on the coral heads where grunts aggregate at daytime. Daytime resting sites are not restricted to corals. In fact, grunts seem to shelter at or near any available structurally complex habitat (i.e., boulders, channel, crevices, mangrove, long-leaved seagrass; Rooker and Dennis 1991, Nagelkerken et al. 2000, Verweij and Nagelkerken 2007). However, similar to nocturnal feeding territories, once established daytime resting sites are used for extended periods. Verweij and Nagelkerken (2007) found that juvenile grunts displayed high site fidelity to daytime resting site core areas of <200 m for >1 yr.

The diel migrations are precisely timed and strongly correlated with changes in light intensity. The migrations to and from the seagrass beds occur at a specific light intensity (McFarland et al. 1979), although the timing is adaptive and can respond to cloud cover-related changes in light intensity. The ‘quiet period’ is an important time window in the twilight migrations of grunts. The ‘quiet period’ is the twilight period between the shelter-seeking of diurnal fishes and the emergence of nocturnal fishes in the evening. In the morning the sequence is reversed. Most fishes are close to the substrate during this period and the activity of crepuscular piscivores peaks because they are visually superior to their prey during twilight periods (Hobson 1972, McFarland and Munz 1976). The juvenile grunts leave the reef before the evening ‘quiet period’ starts and return just after it ends in the morning at identical light intensities.

Many fish exhibit color changes between day and night (Figs. 8.5e, f). In French grunts, color changes are associated with the twilight migration. Unlike white grunts, French grunts migrate in their daytime color dress to and from the reef but forage with a colorless appearance at night which likely provides crypsis in the seagrass (Starck and Davis 1966, McFarland et al. 1979). Thus, the grunts combine foraging and reduced risk of predation while feeding alone in seagrass beds through the night. There is an ontogenetic switch from diurnal to nocturnal activity in juvenile grunts (Helfman et al. 1982), and there are size and age differences in the precision of the diel migration in grunts. Younger specimens (15–30 mm total length) set out later in the evening and return earlier in the morning to the patch reefs (i.e., stay longer in areas of shelter) than larger-sized specimens (40–120 mm). In other words, larger juveniles depart and arrive on the patch reefs in stronger light than the smaller juveniles (McFarland et al. 1979). Similar size-related differences in the timing of twilight activities are known from other marine and freshwater fishes (see Hobson 1972, Helfman 1979, 1981). Factors such as the development of the visual apparatus and predation pressure may lead to less variable diel migration activities with increasing fish size (Helfman et al. 1982). However, Tulevech and Recksiek (1994) found that the twilight migrations of adult *H. plumierii* were less regular than those of juveniles, suggesting that there is a relaxation in the timing of the migratory behavior after maturity.

The start of the nocturnal feeding migration in grunts seems to differ between locations and between grunt species (Rooker and Dennis 1991). In shallow embayments with reduced abundance of piscivores, juvenile grunts still forage during the morning or start foraging in the afternoon in adjacent mangroves or seagrass beds (Rooker and Dennis 1991, Verweij et al. 2006, Verweij and Nagelkerken 2007). McFarland et al. (1979) and Helfman et al. (1982) suggested that piscivores such as lizardfish (Synodontidae) play an important role in shaping the twilight migration of juvenile grunts. This assumption still needs to be tested, e.g., by comparing the migratory patterns of grunts under conditions of higher risk of predation vs. lower risk of predation. Potential experiments might include comparisons of the migratory patterns in marine parks (i.e., higher risk due to more predators) vs. fishing zones (lower risk due to less predators) (see, e.g., Tupper and Juanes 1999), or be based on the older comparison studies of grunts. However, Randall (1963) already mentioned overfishing in the US Virgin Islands. In addition to predation, biological factors such as changes in prey availability, parasite activity, and/or intra- and interspecific competition may influence diel migratory behavior (Helfman 1993).

Active diel migrations follow well-defined pathways between patch reef resting and seagrass feeding sites. The migration routes of smaller specimens persist over several months; those of larger specimens can be re-visited even after years (Ogden and Ehrlich 1977, McFarland et al. 1979). The size-specific stability of migratory routes is likely related to differences in age composition of smaller and larger specimens. The smaller sizes come from a single cohort and cannot rely on experience of others when deciding which migration route to take. The larger grunts are composed of overlapping cohorts, and knowledge of resting sites and migration routes is likely transmitted as a process of social transmission and learning (Helfman et al. 1982, Helfman and Schultz 1984). Quinn and Ogden (1984) provided evidence that juvenile grunts use compass orientation for their regular diel migrations. They concluded that landmarks were unimportant for orientation although they did not explicitly test this. Fish are readily able to generate spatial maps of their environment which are used to guide their movements (Braithwaite and Burt de Perera 2006).

Grunts are primarily obligate diel migrants and dependent on a heterogeneous seascape around reefs. Their diversity and abundance is reduced where either diurnal shelter sites or back-reef forage habitat are lacking (Starck and Davis 1966 p. 352, Gladfelter et al. 1980, Baelde 1990). Although grunts are mobile species, they display high site fidelity to feeding and shelter core areas. This makes them considerably vulnerable to selective small-scale habitat change, e.g., the loss of particular patch reefs or single mangrove stands.

8.4.2 Other Families and Species

The diel migrations of a few other species have been studied in some detail (Table 8.1). *Pempheris schomburgkii* (Pempheridae) in St. Croix (US Virgin Islands) migrate around sunset from daytime back-reef refuges to nocturnal fore-reef feeding sites (Gladfelter 1979). At sunset, a complex sequence of behaviors begins (e.g., appearance at crevice entrance, ‘flashing’, ambivalence, emergence, aggregation, swimming along pathways) which takes the schools along complex pathways to the fore-reef where groups split off and fishes forage for meroplanktonic crustaceans singly or in small groups through the night. In the morning, *P. schomburgkii* return along the same pathways but at lower light levels. *Acropora* landmarks are important, and the timing is age-specific and triggered by light intensity, similar to grunts. The twilight migration covers distances of almost 1 km but is limited to the reef structure.

Likewise, Apogonidae maintain daytime resting sites close to reef structures from where they migrate to nocturnal feeding grounds in different near-reef habitats such as open water, sand, seagrass habitats, and the reef proper, partitioning niches spatially (Collette and Talbot 1972, Vivien 1975, Marnane and Bellwood 2002). They may return to the same resting sites each morning for months or years (e.g., Kuwamura 1985, Okuda and Yanagisawa 1996, Marnane 2000, Ménard et al. 2008) and thus regularly transport nutrients and energy to and from their reefal resting sites. However, their foraging range is relatively short (30 m in Marnane and Bellwood 2002).

Hobson (1968) was able to chart the evening route of *Harengula thrissina* (Clupeidae) in the Gulf of California which took the fish more than 500 m offshore. In the Marshall Islands, *Pranesus pinguis* (Atherinidae) rested in schools nearshore during the day and followed ‘the same route each evening’ to disperse offshore and feed on plankton up to 1.2 km away from the diurnal schooling sites (Hobson and Chess 1973). In Hawaii, the mullid *Mulloides flavolineatus* formed daytime resting schools and moved distances between 75 and 600 m to nearby sand flats to forage (Holland et al. 1993). Site fidelity was extremely high. Individuals were recaptured after up to 531 days. The foraging range was restricted to $\sim$ 13–14 ha (own estimate from a map in Holland et al. 1993). Acoustically-tagged *Parupeneus porphyreus* (Mullidae) showed consistent diel patterns of behavior, taking refuge in holes in the reef by day and moving over extensive areas of sand and coral rubble habitat at night (Meyer et al. 2000).

In the Caribbean, juvenile snappers such as *Lutjanus apodus* also carry out twilight migrations from their daytime resting sites in mangroves or protected rocky shorelines (Verweij et al. 2007) to nighttime soft bottom foraging grounds, such as seagrass beds (Starck and Davis 1966, Rooker and Dennis 1991, Nagelkerken et al. 2000). Nocturnal Lutjanidae might be important predators of foraging Haemulidae at night (Starck and Davis 1966). Acoustic tracking of lane snapper *L. synagris* on St. John (US Virgin Islands) showed sun-synchronous nocturnal migrations with a regular departure from the eastern side of the Lameshur Bay after sunset and a return before sunrise, and strong daytime site fidelity for a period of 268 days (Fig. 8.7).

Similar twilight migrations can also be observed on the Pacific coast of Colombia (G Castellanos-Galindo, Universidad del Valle, Colombia, pers. comm.). Evidence for short-term migrations is often inferred from day-night shifts in species compositions at given sites or accidental observations, but real-time tracking of movements and behavior remains insufficient. Portable GPS tracking of *L. decussatus*

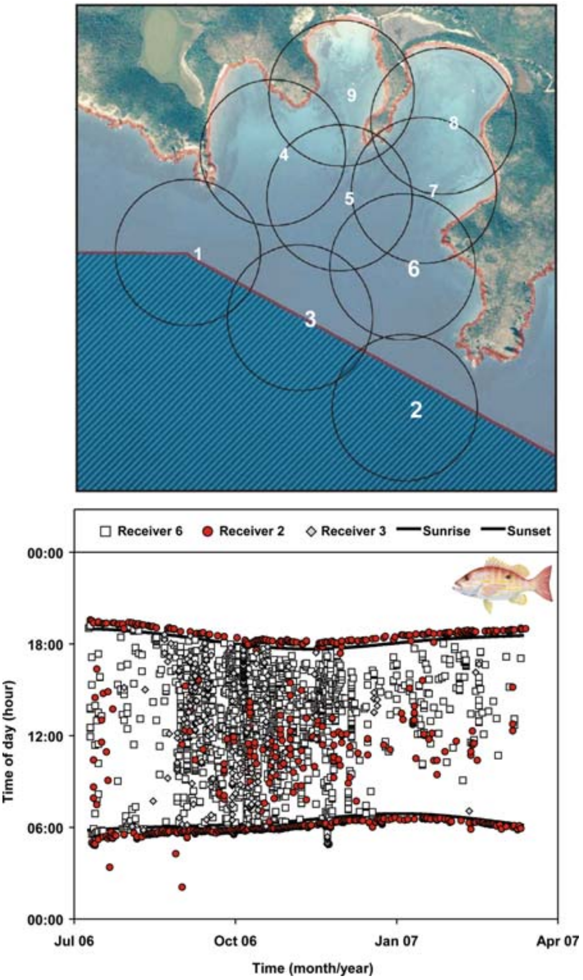

Fig. 8.7 Plot of receiver detections for an individual lane snapper (*Lutjanus synagris*, 29 cm total length) at Lameshur Bay, St. John (US Virgin Islands) between 12 July 2006 and 5 April 2007 (bottom graph). Upper figure: locations of nine receivers in the bay showing the 300-m-radius detection buffer (circles) and station detection overlap. Receiver 6: inner bay site with patchy seagrass at 17 m water depth; receiver 2 and 3: outer bay sites at ∼ 22 m water depth. Adapted from Friedlander and Monaco (2007), with kind permission of S Pittman (NOAA). Fish artwork commissioned from D Peebles by Florida Fish and Wildlife Conservation Commission

during daylight hours in an Okinawan coral reef revealed high daytime site fidelity (Nanami and Yamada 2008). The size of daytime home ranges ranged between 93 and 3638 m^2.

8.4.3 Feeding Guilds

Diel activity seems to have a strong phylogenetic background and may be a familial characteristic (Helfman 1993). Since the species of many fish families feed on similar food organisms, a generalization of the diel migrations in terms of feeding guilds is possible. Note, however, that fish are opportunistic, and activity patterns can vary in response to numerous biological and abiotic factors.

Nocturnal invertebrate feeders usually migrate from daytime shelter at dusk, feed through the night, and return to seek cover at dawn (e.g., Haemulidae, Mullidae). Seagrass beds are often preferred as nighttime habitats because during darkness invertebrate abundance is high (e.g., Robertson and Howard 1978), and higher than in adjacent habitats (e.g., Nagelkerken et al. 2000). However, French grunts, for example, are facultative nocturnal foragers and were observed feeding also at daytime in mangrove and seagrass beds (Verweij et al. 2006).

Herbivores are clearly diurnal (Pomacentridae, Scaridae) (Helfman 1993). The latter feed on seagrass, and also on coral and filamentous algae growing on dead coral rock during daytime, and hide in the reef at night (Ogden and Zieman 1977). If moonlight is sufficient, herbivores may also be active at night (Hobson 1965).

Piscivores may adopt one of two strategies. They can hide in the reef at daytime, emerge after the ‘quiet period’, roam from reefs into seagrass meadows and forage at night (e.g., moray eels, snake eels, Lutjanidae). They can also show opportunistic behavior with activity at day and/or night in response to prey availability (e.g., Sphyraenidae or Carangidae in the Caribbean, Ogden and Zieman 1977; Lutjanidae, Belonidae, and Carangidae in Pacific Colombian rocky shores, G Castellanos-Galindo, Universidad del Valle, Colombia, pers. observ.).

Zoo- and phytoplanktivores usually aggregate in dense, relatively inactive reef-associated schools to fan out from their reefal resting sites in the horizontal and vertical scale to search for food in the adjacencies. At dusk, schools of nocturnal planktivores such as Apogonidae or Pempheridae disperse to feed at night, often after moving a considerable distance offshore (Hobson 1965, Fishelson et al. 1971). At dawn, diurnal planktivores such as Pomacentridae disperse and forage on near-reef plankton. It is debatable whether the reefal migrations and those of many other families and species mentioned in Table 8.1 really connect different ecosystems, or whether they are movements in the reef–sand interface and restricted to the sphere of influence of a reef. Nevertheless, these movements lead to the regular transfer of non-reef production to the reefal resting sites and may thus in fact be considered diel migrations between adjacent ecosystems.

8.5 Diel Movements of Decapods

In the marine realm the order Decapoda is represented by three groups: shrimps, lobsters, and crabs (Ruppert and Barnes 1994). Given the differences in their biology, the groups are treated in order following their ability to swim, which may affect the potential to make extensive diel movements.

8.5.1 Lobsters

After settlement, lobsters are benthic animals and avoid swimming. Our knowledge on short-term movements of lobsters mainly stems from clawed (Nephropidae and Homaridae) and spiny lobsters (Palinuridae) that are remarkably similar in morphology, ecology, and behavior. Lobsters are mostly nocturnal. They spend most of their daytime sheltering in subtidal crevices and caverns of reefs and erosional edges of seagrass patches (‘blowouts’), and leave their dens at night to forage in surrounding areas (e.g., Herrnkind 1980, Cobb 1981, Joll and Phillips 1984, Phillips et al. 1984, Jernakoff and Phillips 1988, Jernakoff et al. 1993, Acosta 1999). Where different ecosystems form a heterogeneous seascape, nightly walks clearly connect adjacent ecosystems.

Detailed studies come mostly from subtropical or temperate coasts. For instance in Western Australia, *Palinurus cygnus* leave their dens at night and forage in the seagrass beds around the reefs (Cobb 1981). Home range sizes are usually <500 m and lobsters display high site fidelity. Juvenile *P. cygnus* forage over small areas, usually within a 20 m radius, but sometimes as far as 50 m from their den (Chittleborough 1974). Juvenile *P. cygnus* usually move at a rate of ca. 1 $m.min^{-1}$ at night. When walking over bare sand, they travel at speeds of up to 18 $m.min^{-1}$ (Jernakoff 1987). Similarly, in the tropics subadult *P. argus* walked between 25 and 416 m overnight, and distances walked were similar after one week (Lozano-Alvarez et al. 2003). The emergence patterns, however, change ontogenetically. Early benthic-phase *P. argus* (<15 mm carapace length CL) rarely leave their shelters, juveniles (30–62 mm CL) leave their shelter 2–30 times per night, usually with excursions of <10 min, and adults (>80 mm CL) walked ‘for extended periods of time during the night’ (Weiss et al. 2008). The home range of *P. guttatus* ranges within a radius of 100 m (Lozano-Alvarez et al. 2002). All *P. versicolor* were recaptured within 500 m of their original den (Frisch 2007).

Foraging activity varies between sexes and size groups (Weiss et al. 2008). The activity is constant throughout the night (Jernakoff 1987, Frisch 2007), displays peaks, often in the hours after sunset (e.g., Fiedler 1965), or ceases several hours before dawn when the lobsters return to their dens (Herrnkind 1980). While walking through their home range, the lobsters use geomagnetic fields, water movements (Creaser and Travis 1950, Herrnkind and McLean 1971, Lohmann 1985), and structural cues such as blowouts for orientation (Cox et al. 1997).

Light levels and turbidity at the onset of light or darkness seem to control the movements (Herrnkind 1980). *Jasus lalandii* feed at maximum rate a few hours after sunset, closely matching the locomotory patterns (Fiedler 1965). In juvenile *P. cygnus* most foraging activity begins in response to changes in light levels associated with dusk and not by diurnal changes in water temperature or currents. Similarly, juvenile lobsters return from foraging at about dawn when light levels begin to increase (Jernakoff 1987).

Juvenile lobsters are likely important predators; their feeding ecology probably affects the structure of the benthic community in their home range (Joll and Phillips 1984), but due to their mixed and diverse diet (e.g., Briones-Fourzan et al. 2003) it is difficult to quantify their contribution to overall trophic flows.

Nightly forays of lobsters can be restricted to a single reef (e.g., Chittleborough 1974) or can include traveling to reefs several kilometers away where they stay for some time before returning to the original home range (Herrnkind 1980). These movements, however, seem to be infrequent and usually below 20 km (Trendall and Bell 1989). Vegetated substrates may function as movement corridors between insular habitats and facilitate dispersal, besides being important settlement areas. Consequently, protection of areas with a heterogeneous and vegetated seascape is important to fulfill the changing requirements of species with a complex life cycle, such as lobsters (Acosta 1999).

8.5.2 Penaeid Shrimps

Shrimps are usually bottom dwellers and intermittently use their pleopods to swim. Burial and activity of penaeid shrimps is influenced by (1) the diel cycle, (2) moonlight, (3) turbidity, and (4) the tidal cycle (Dall et al. 1990). The typical life cycle of penaeid shrimps connects the offshore areas (adult stock, reproduction) with the innermost areas of estuaries and embayments (nursery ground) (see Chapter 7). Short-term movements that connect different shallow-water ecosystems are restricted to the postlarvae and juvenile stage in the nursery grounds.

If regular diel movements of shrimp connect adjacent ecosystems, their activity patterns most likely follow one of three light-dependent activity types that Penn (1984) classified according to the shrimps' burrowing behavior. (1) Shrimps in clear water may burrow at day or in bright moonlight and emerge only at night. (2) Shrimps in slightly turbid water may be nocturnal but occasionally emerge during the day. (3) Shrimps in more turbid water seldom if ever burrow. The home range size of individual shrimps after settlement in a nursery ground has rarely been identified, most likely due to obvious problems in mark-recapture experiments (see Schaffmeister et al. 2006). Evidence for short-term movements between adjacent ecosystems by shrimps mainly comes from tidal coasts (see Section 8.8.2).

8.5.3 Crabs

Most crabs cannot swim and their benthic movements are unlikely to regularly connect adjacent ecosystems. Portunid crabs, however, are agile swimmers. The last pair of legs terminates in paddle-like swimming legs. The legs resemble figure eights in their movement, similar to a propeller. The forth pair of legs counter-beat and act as stabilizers. Nevertheless, they are mostly benthic and swim only intermittently (Ruppert and Barnes 1994). Information is available primarily from commercially important species. In a South African estuary with a maximum tidal range of 1.4 m, nocturnal foraging movements of the subtidal mud crab *Scylla serrata* ranged from 219–910 m (Hill 1978). Interactions of the movements with the tidal cycle were not mentioned. They tended to stay in the same general area although they were capable of moving at least 800 m along the length of the estuary at night (Hill 1978). By continuously shifting their general area, mud crabs can cover distances of several kilometers within a few weeks (Hyland et al. 1984). Thus, mud crabs are readily able to connect adjacent ecosystems but no attention has been paid as to whether this occurs on a regular diel or tidal basis.

The blue swimmer crabs *Portunus pelagicus* are opportunistic, bottom-feeding carnivores and scavengers (Kangas 2000). They are most active in foraging and feeding at sunset (Grove-Jones 1987, Smith and Sumpton 1987, Wassenberg and Hill 1987). Although *P. pelagicus* generally forage in the habitat in which they rest diurnally, they readily move to other habitats and have a wide-ranging foraging strategy (Edgar 1990). Due to their strong swimming ability, *P. pelagicus* are capable of moving substantial distances, with one recorded as traveling 20 km in one day in Moreton Bay, Queensland (Sumpton and Smith 1991). However, tagging studies in Moreton Bay showed that small-scale movement of crab populations are more common. Of the recaptures, 79% were caught <2 km from their release points, and only 4% were recaptured >10 km from their release point (Potter et al. 1991). Similarly, recaptures within 4 km of release sites have occurred for *Scylla serrata* (Hyland et al. 1984) and *Callinectes sapidus* (Mayo and Dudley 1970). Feeding of *C. arcuatus* in Pacific Mexico occurs mostly at dusk (Paul 1981). *Thalamita crenata* in Kenya forages both during the day and night, however, in significant interaction with the tidal cycle (Vezzosi et al. 1995, Cannicci et al. 1996). Unfortunately, detailed biological information for many other portunid species of the genera *Charybdis*, *Portunus*, *Scylla*, and *Thalamita*, particularly from Southeast Asia, is not available.

In conclusion, there are no accounts of synchronized short-term mass movements of decapods to particular habitats from any tropical coast with weak tides that are comparable to the diel migrations reported for numerous reef fish families and species. However, the diel movements of lobsters unambiguously connect adjacent ecosystems. The putative connectivity between adjacent ecosystems by diel migrations of shrimps and portunid crabs still awaits more robust evidence. The timing of diel movements in shallow-water decapods is also related to the twilight period but compared to fish, the movements seem to be less strictly structured in time. Overall diel foraging ranges of lobsters, and particularly of portunid crabs, can be similar to those of fish.

8.6 Tidal Movements of Fish

On marine coasts, diel activity is usually tightly coupled to the additional stimulus of the tides. On coasts with low tidal range, e.g., the Red Sea or the Caribbean, the activity patterns of fishes are primarily synchronized with the day-night cycle (see Section 8.4). On most other coasts, rhythmic behavior of the coastal organisms is synchronized more strongly with the tide, but still in close interaction with the diel cycle (Gibson 1993). The few studies available on fish species that live on both tidal and non-tidal coasts have shown that the rhythmic behavior reflects the relative importance of the tide in their respective environment (the gobiid *Pomatoschistus minutus*, the pleuronectid *Platichthys flesus*: Gibson 1982; the ariid *Arius felis*: Steele 1985, Sogard et al. 1989).

Previous reviews on tidal movements of fish have focused on rocky shores, sandy beaches, saltmarshes, or migrations in the open sea (Gibson 1969, 1982, 1988, 1992, 1993, 1999, 2003, Kneib 1997, Harden Jones 1968, Metcalfe et al. 2006). These reviews refer mostly to the higher latitudes of the northern hemisphere but their findings provide a robust background to investigate the tidal movements of tropical shallow-water fishes. References from outside the tropics are cited whenever examples from the tropics are unavailable.

8.6.1 Transients and Residents

Intertidally migrating fish transport energy from the intertidal into the subtidal area, both short-term and long-term (e.g., seasonal emigration or ontogenetic movements, see Chapter 6). Therefore, the sublittoral is treated here as an ecosystem different from the intertidal, and virtually all intertidal migrants are considered to connect different ecosystems.

Gibson (1969, 1988) classified intertidal fishes into residents (fish that live in the intertidal) and transients (temporary visitors during times of intertidal inundation that return to the subtidal). He further classified the transients according to the regularity of intertidal use into tidal, lunar, seasonal, and accidental visitors. The residents are not considered in this section because their movements do not connect adjacent ecosystems. In contrast to the intertidal migrants that move up and down the shore with the rise and fall of the tide (i.e., strong upshore component), there are the subtidal migrants which principally use tidal currents to move between subtidal habitats and avoid entering the intertidal zone (i.e., strong alongshore component). These classifications, however, have smooth transitions. Migratory patterns can differ between individuals, size groups, sexes, species, and populations (Gibson 1999, 2003), resulting in complex patterns of seascape use by mobile organisms.

8.6.2 Tidal Migrations in Tropical Habitats

During high tide, transients make temporary use of a wide range of accessible tropical habitats. When immersed, numerous fish colonize mangroves and mangrove-lined creeks (e.g., Robertson and Duke 1987, Little et al. 1988, Chong et al. 1990, Robertson and Duke 1990, Sasekumar et al. 1992, Laroche et al. 1997, Kuo et al. 1999, Rönnbäck et al. 1999, Tongnunui et al. 2002, Krumme et al. 2004, Vidy et al. 2004) and mudflats (e.g., Abou-Seedo et al. 1990, Chong et al. 1990). Transient fish move onto sandy beaches (e.g., Brown and McLachlan 1990, Abou-Seedo et al. 1990, Yamahira et al. 1996) and forage on rocky shores (e.g., Castellanos-Galindo et al. 2005, Gibson 1999). In Australian seagrass beds, midwater feeders move from adjacent habitats to the water column above the seagrass at high tide (Robertson 1980). The rock flathead *Platycephalus laevigatus* use seagrass beds together with their main prey *Nectocarcinus integrifons* during nightly or evening high tides (Klumpp and Nichols 1983). Sogard et al. (1989) inferred from continuous gill net catches that fish moved in seagrass banks primarily around high tide in Florida Bay, USA. On the Marshall Islands, Central Pacific, Bakus (1967) observed the mass migration of algal grazing surgeonfish (*Acanthurus triostegus, A. guttatus*) on and off reef flats with the tide. The herbivorous surgeonfish *A. lineatus* re-established intertidal territories each morning on a reef flat in Samoa (Craig 1996). At some sites in the Gulf of Aqaba, schools of the surgeonfish *A. nigrofuscus* migrated daily on a routine pathway 500–600 m from nocturnal reefal resting sites to intertidal daytime feeding sites (Fishelson et al. 1987). In South Sulawesi, Unsworth et al. (2007b) assumed that *Caranx melampygus, Hemiramphus far,* and *Lutjanus* spp. moved from reef to seagrass habitat at high tide. Bray (1981) observed large *Chromis punctipinnis* consistently foraging at the incurrent end of a reef in southern California and moving to the opposite end of the reef when the current turned.

8.6.3 Functions of Intertidal Migrations

Feeding (function 1) and shelter (function 2, i.e., avoidance of predation) are likely the two most prominent functions of tidal movements (Gibson 1999). Tidal migrations often connect low-water resting sites with high-water feeding sites. Most transient fish seem to enter the intertidal with the flood tide, feed around high tide, and return at ebb tide to subtidal resting sites, thereby avoiding stranding (Robertson and Duke 1990, Krumme et al. 2004). During low tide the fish rest and digest. Differences in the local environmental settings, such as intertidal habitat accessibility, may influence the importance of intertidal feeding grounds. Results from Lugendo et al. (2007) suggest that mangroves close to subtidal resting areas (mangrove-lined creeks) are more important feeding sites for fishes than mangroves that drain completely (fringing mangrove).

Figure 8.8 illustrates the intertidal migration of the four-eyed fish *Anableps anableps*. The fish ride the early flood tide towards the upper reaches of mangrove-lined creeks where they feed around high tide. The fish return with the late ebb tide to the subtidal channel where they rest near the channel banks through the low-water period (Brenner and Krumme 2007). Amphibious mudskippers (Gobiidae) show a reverse tidal migration pattern; they rest at high tide, move downshore at ebb tide, and feed during the low-tide period to again retreat at flood tide (e.g., Colombini et al. 1996).

Examples from temperate coasts show that the rhythmic pattern of ingestion in transients is reflected in quantitative changes, with fuller stomachs at ebb tide vs. flood tide (e.g., Weisberg et al. 1981, Kleypas and Dean 1983, Hampel and Cattrijsse 2004), and in qualitative changes during tidal cycles (Ansell and Gibson 1990). During high tide the intertidal accessibility and visibility peak, and slower current speeds likely facilitate maneuvering, particularly for benthic invertebrate feeders and herbivores (Brenner and Krumme 2007). In addition to high-tide feeding, phyto- and zooplanktivores may take advantage of plankton naturally concentrated at low tide, e.g., in dead-ending channels (Krumme and Liang 2004). Likewise, piscivores may feed primarily during ebb tide at the mouths of creeks and channels, preying upon returning fish. Hoeinghaus et al. (2003) inferred such a strategy for piscivores from samples taken in the Venezuelan floodplains.

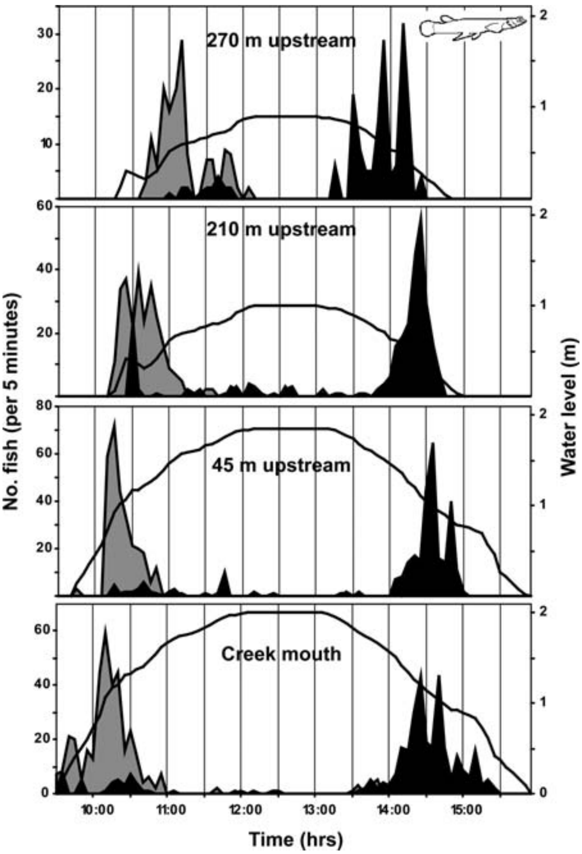

Fig. 8.8 Intertidal migration of the surface-swimming four-eyed fish *Anableps anableps* in a mangrove creek in north Brazil (neap tide, 29 June 2005). Simultaneous visual censuses on four transects of increasing distance upstream from the creek mouth (bottom to top). Falling water levels (solid lines) and decreased duration of inundation reflect topographic height of transect. Grey: upstream fish movements, black: downstream fish movements. Note different Y-axes (U Krumme, unpubl. data)

Fish swimming in shallow water reduce the risk of predation by piscivores which also enter at flood tide from deeper waters (e.g., Ruiz et al. 1993). Transients may move to high-tide sites to avoid predation in the area occupied during low tide (e.g., Dorenbosch et al. 2004). Reduction of the risk of predation is suggested when mouth-breeding and fasting male catfish *Cathorops* sp. only enter the intertidal at evening spring tides (Krumme et al. 2004) or – an example from a temperate coast – when fish move to the intertidal although the food supply is richer in the subtidal (Ansell and Gibson 1990).

Convincing evidence is lacking for tidal migrations (function 3) of fish as the result of inter- or intraspecific competition (see, e.g., Hill et al. 1982 for an example of the swimming crab *Scylla serrata*). In field experiments, it will be difficult to exclude the potential effect of piscine predators on differences between species or age groups.

Besides using the intertidal for feeding and shelter, several species carry out tidal migrations (function 4) to spawn (see Gibson 1992, 1999, De Martini 1999) or undertake regular small-scale or seasonal larger-scale movements to spawning sites, often following the lunar or spring tide cycle (e.g., Shapiro 1987, Zeller 1998; Chapter 4). A fifth function of tidal movements, the search by fish for physiologically appropriate environmental conditions (Gibson 1999), remains unclear because changes in water temperature, salinity, or oxygen content are highly correlated with tidal changes in water level. In the tropics, water temperature fluctuations are relatively small and estuarine fish are mostly euryhaline. Extreme salinities or hypoxia usually build up gradually and fish try to move out from affected areas, however, not necessarily with the tide (e.g., Shimps et al. 2005).

8.6.4 Sequence of Species and Size Groups

The little evidence available suggests that the intertidal movements of dominant nektonic organisms during flood and ebb tide are structured, both on the species level and among size groups. Inter- and intraspecific differences in factors such as minimum water level requirements, the relative location of the low-water resting sites, presence of predators, or foraging efficiency in the intertidal may lead to an ordered sequence of species and size groups entering and leaving the eulittoral. The most robust results come from eastern US saltmarsh creeks. Kneib and Wagner (1994) found that the number of species and individuals generally peak at high tide in flume weir samples compared to shallow flood and ebb tide samples. Their data suggested that smaller fish and shrimp travel shorter distances onto the marsh than larger conspecifics. Bretsch and Allen (2006a) used a sweep flume to quantify the migrations of nektonic species into and out of saltmarsh intertidal creeks. The migrations were nonrandom and structured; residents entered early at flood tide while transient species entered later at higher water levels. A species' water depth at peak migration increased as the species grew during summer. For north Brazilian mangrove creeks, Krumme et al. (2004) suggested that the emigration routes of the mangrove creek transients split inter- and intraspecifically at ebb tide, and took different species and life stages to specific resting sites. Data of Giarrizzo and Krumme (unpubl.) show that smaller *Colomesus psittacus* (Tetraodontidae) enter earlier at flood and leave later at ebb tide than larger conspecifics. Similarly, the youngest four-eyed fish *Anableps anableps* immigrate a few minutes earlier and return at few minutes later at lower water levels than the larger specimens (U Krumme unpubl. data). Thus, the more vulnerable and smaller fish maximize the time spent in the intertidal. It remains to be tested whether the smaller sizes stay longer to avoid predation or because they are still less efficient foragers.

8.6.5 Cues of Tidal Migrations

Tidal migrations are precisely timed, to achieve movement in appropriate conditions at flood tide and to avoid stranding when the tide recedes. The outcome of studies can differ considerably depending, e.g., on when and where samples are taken and what type of sampling gear is used (Gibson 1999). Knowledge about the cues fish use to migrate with the tide is crucial to define replicable sampling intervals in accordance with parameters relevant to the fish. Experiments have shown that fish respond to changes in underwater pressure (Gibson 1971, 1982, Gibson et al. 1978), fluctuations in water level (Ishibashi 1973), and hunger state (Nishikawa and Ishibashi 1975). Temperate flatfish may migrate with the tide by simply maintaining a constant depth (Gibson 1973). Bretsch and Allen (2006a) found that species use the same water depth to enter and leave the creeks, thus supporting Gibson's hypothesis. Likewise, the tidal migration of *Anableps anableps* is controlled by water level and not by a particular time interval before or after high or low tide (Brenner and Krumme 2007) (Fig. 8.8). Bretsch and Allen (2006b) further showed experimentally that mummichog (*Fundulus heteroclitus*) and grass shrimp (*Palaemonetes* spp.) selected shallower water depths to migrate in the presence of other predatory and non-predatory fish species, i.e., the timing of tidal migrations was in response to abiotic factors and to multiple-taxa effects, e.g., in attempts to reduce the risk of predation (Gibson and Robb 1996). Most likely tidal transients use several cues, both abiotic and biotic, simultaneously. The influence of other possible tide-related stimuli such as current speed, temperature, the sound generated by the current, or other biotic interactions awaits experimental testing.

To ensure comparability between samples, it is necessary to sample at slack low water and/or high water when assemblage compositions are most stable. Flood and ebb tides are fairly dynamic periods when the nektonic community is reshuffled. Sampling at flood or ebb tide likely increases variation and can lead to unwanted bias.

Studies that comparatively evaluate habitat types should take samples both at high and low tide in all habitat types to avoid results biased by tidal movements. For instance, high-tide samples from adjacent mangrove and seagrass habitats may suggest that mangroves support higher fish biomass than seagrass beds, but in actuality the fish may use the seagrass bed at low tide – which may result in higher low-tide fish biomass in the seagrass habitat – and move to the mangroves at high tide.

8.6.6 Movements and Foraging Ranges

The intertidal movement patterns and foraging ranges are of particular interest in attempts to identify appropriate marine park limits. Knowledge of the tidal movements of tropical fish is scarce. In Hawaiian atolls, the top predator *Aprion virescens* (Lutjanidae) was seasonally site-attached to core activity areas of up to 12 km in length, and ranged up to 19 km across atolls. Within their core areas, tagged *A. virescens* exhibited diel and tidal habitat shifts, with the latter resulting in round trips of up to 24 km in 24 hrs despite a tidal range <1 m (Meyer et al. 2007a). Fish moved along the barrier reef at flood tide and returned at ebb tide. A similar home range size of up to 29 km per day was determined for giant trevally *Caranx ignobilis* (Meyer et al. 2007b). The Hawaiian atolls lack vegetated ecosystems so that the fish do not migrate between mangroves and seagrass habitats, but the studies highlight the relatively broad scale of movements that subtidal top predators can cover during short-term migrations, even in microtidal areas.

In examples from temperate estuarine species, ultrasonically-tagged flatfish covered distances from 0.1–1.5 km (Wirjoatmodjo and Pitcher 1984, Szedlmayer and Able 1993) while *Liza ramada* (Mugilidae) even covered a median distance of 6,245 m during a complete tidal cycle (Almeida 1996). When tidally migrating, the fish may use selective tidal stream transport at flood or ebb tide (Forward and Tankersley 2001). Kleypas and Dean (1983) and Krumme (2004) showed that intertidal fish ride the flood tidal currents to arrive at their foraging grounds.

Strong tidal currents can also limit the activity of fishes. *Labroides dimidiatus* (Labridae) adapted the position of its cleaning station in response to tidal currents (Potts 1973). Flatfish such as *Pleuronectes platessa* bury in the sediment when currents are too strong (Arnold 1969).

8.6.7 Site Fidelity and Homing

Given the dynamics of the tides, one could suggest that fish on tidal coasts are organized in ‘mobile stocks without attachment to particular locations’ (Sogard et al. 1989). Evidence is mounting, however, that shallow-water fish center their short-term activities in core areas, display site fidelity, and home to familiar sites. This makes the fish particularly vulnerable to local exploitation on the one hand, but also likely to receive adequate protection with the establishment of no-fishing zones on the other. Knowledge of the surrounding seascape structure and topography is certainly beneficial for the fish to optimize the use of resting and feeding sites in complex environments. Fish may use physical features such as landmarks to navigate in a complex dynamic 3d-environment (Gibson 1999, Braithwaite and Burt De Perera 2006, Brown et al. 2006). Dorenbosch et al. (2004) suggested homing and site fidelity in tagged juvenile *Lutjanus fulviflamma* and *L. ehrenbergii* in Zanzibar. During daytime the fish apparently moved with the tide from a low-tide to a high-tide resting habitat (channel to notches), probably to avoid predation. Fishelson et al. (1987) and Craig (1996) provide evidence for site fidelity to high-tide feeding sites in reef systems (see also McFarland and Hillis 1982, Kuwamura 1985, Okuda and Yanagisawa 1996, Marnane 2000, Beets et al. 2003).

8.7 Comparison Between Diel and Tidal Migrations

8.7.1 Analogies and Differences Between Diel and Tidal Migrations

From the aforementioned patterns in diel and tidal migration it has become apparent that there are remarkable analogies between these short-term migrations, but

Table 8.2 Analogies and differences between diel and tidal migrations in fish[a]

	Feature	Diel migration[b]	Tidal migration[c]
Analogies			
1	Resting site	Structurally complex habitats	Subtidal, low water
2	Feeding site	Reef adjacencies (seagrass, sand, etc.)	Intertidal, high water
3	Migration period	Dusk and dawn	Flood and ebb tide
4	Sequence in species	Yes, according to light intensity	Yes, according to water depth
5	Sequence in size groups	Yes	Yes
6	Smaller stay longer in shelter	i.e., resting site	i.e., intertidal zone
7	Site fidelity	Resting and feeding sites	Resting and feeding sites
8	Homing	Yes	Yes
9	Migratory pathways	Constant over time	Constant over time
Differences			
1	Timing	Light intensity	Tidal cues and light intensity
2	Movements	Active	Partly gratis; riding the tide, selective tidal stream transport, active
3	Duration of migration	Short (min); twilight periods	Longer (hrs); flood and ebb tide
4	Predictability	Temporal variation lower	Temporal variation higher
5	Max. no. of migrations day^{-1}	One	Two (semidiurnal tide)
6	Foraging range	A few 100 m, rarely >1 km	Several 100 m to a few km

[a] Transients *sensu* Gibson (1969, 1988)

[b] Pure diel migrations are restricted to coasts with negligible tidal range (Caribbean, Red Sea, oceanic islands, and several areas in South and Southeast Asia; see Section 8.3)

[c] On all other coasts the tidal and diel cycles are tightly coupled

that there are also differences (Table 8.2). The analogies (numbered 1–5 below) certainly do not apply to all species, size groups, and locations, but the comparison may emphasize underlying constituents of short-term migrations subject to different ambient cycles.

(1) Both diel and tidal migrations usually connect resting areas with feeding areas. In diel migrations which only occur on coasts with weak tides, the fish rest at daytime and forage at night or vice versa, whereas in tidal migrations fish usually rest at low tide and forage at high tide.
(2) The structurally complex resting sites of diel migrants (e.g., caves, crevices, or mangroves) may correspond to low-water resting sites in the subtidal (burial in soft sediment, shelter in subtidal structure). Subtidal structure provided by dead plant material (Daniel and Robertson 1990) or vegetation such as seagrass can provide significant benefits to tidally migrating species (Irlandi and Crawford 1997).

(3) The diel migrations at sunset and sunrise may correspond to the immigration at flood tide which takes the fish to their foraging grounds, and the emigration at ebb tide which takes them back to their resting sites.
(4) Diel and tidal migrations are characterized by a sequence of species and size groups in the departure from and return to resting sites. Different species and size groups have different requirements and respond differently to changes in light intensity or water depth which results in temporally and spatially more or less structured short-term migrations. Smaller diurnal individuals and species returned earlier to nocturnal resting sites at dusk and emerged later at dawn than larger individuals and species (Hobson 1972, Helfman 1981). In nocturnal species, smaller size-groups migrated at lower light levels (McFarland et al. 1979). In tidal migrations, smaller individuals or species often travel at shallower depths than larger species and size groups. In general, smaller individuals seem to stay longer in the shelter site than larger individuals, either in the resting site or in the inundated littoral. Ontogenetic changes in the risk of predation seem to be reflected in the timing of both diel and tidal migrations.
(5) Site fidelity, homing, and constant migratory pathways, i.e., the use of core areas, has been evidenced in both diel and tidal migrations. Knowledge of the surrounding seascape structure is certainly useful to optimize shelter use and food search.

Differences between diel and tidal migrations (numbered 1–6 below) are apparent and mostly related to the different durations and physical features of the underlying cycles (Table 8.2).

(1) Changes in light intensity trigger diel migrations, whereas tidal cues control tidal migrations. On tidal coasts, primarily diurnal species center their foraging activities on daytime high tides, and nocturnal species on nightly high tides.
(2) The twilight migration is a relatively short event, often completed in <0.5 hr, whereas the movements to and from the intertidal foraging grounds may last more than 1 hr at flood and ebb tide, respectively.
(3) In diel migrations the distance between resting and feeding sites has to be covered by active swimming. Tidal migrations also involve active movements but are significantly facilitated by the tidal conveyor belt. Fish may ride the tide and use selective tidal stream transport to move to their destinations. Locomotory expenditure is reduced and saved energy can directly be transferred into increased growth and survival.
(4) Due to the relatively constant diel cycle in the tropics, diel movements are highly predictable but restricted to the relatively short twilight period, and therefore movements are precisely timed and show low variation. In contrast, the tidal cycle is subject to considerable variations due to astronomical, meteorological, and topographical reasons. Therefore, patterns in tidal migrations are likely more variable and more difficult to untangle than those of diel migrations.
(5) Diel migrations are restricted to dusk and dawn so that only one round trip per day is possible. Tidal migration on semidiurnal coasts can be carried out up to twice daily.

(6) Given our current knowledge, the foraging range of diel migrations may extend a few 100 m from the resting sites, sometimes exceeding 1 km, but are rarely larger than 2 km. Much less is known about foraging ranges of tidally migrating species but evidence suggests that distances are larger, maybe by one order of magnitude. Fish seem to travel distances of several 100 m to several kilometers each tide. It is remarkable that Hawaiian reef top predators move >20 km per day with the tide despite a tidal range of only 1 m.

8.7.2 Spring–Neap Tide Alternation

One feature characterizing tidal migrations but lacking in diel migrations is the spring-neap tide alternation. The quasi-weekly pulse of greater and smaller tidal ranges and current speeds is likely to have profound consequences for intertidal organisms. Tidal coasts are characterized by a vertical zonation of benthic organisms. The higher the tide, the more vertical zones are accessible and the more profitable is a visit by intertidal transients, and vice versa. Consequently, at spring tides usually more fish use the intertidal area than at neap tides (e.g., Davis 1988, Laegdsgaard and Johnson 1995, Wilson and Sheaves 2001, Krumme et al. 2004). The possibility of more extensive tidal migrations during spring tides was referred to above (see Section 8.3). The spring-neap tide cycle is reflected in cycles of food intake (e.g., Colombini et al. 1996, Brenner and Krumme 2007, Krumme et al. 2008), growth in intertidal fish (Rahman and Cowx 2006), and likely in cycles of mortality in the prey organisms. Thus, many tidal coasts are systems of two states, characterized by their different levels of tidal disturbance (Brenner and Krumme 2007). At neap tides the interaction between system compartments is relatively low (low inundation and low current speeds) compared to the highly dynamic spring tide periods (high inundation high and current speeds).

Mangrove coasts feature an additional transport mechanism for nearshore organisms. Floating mangrove litter is exported particularly during spring ebb tides (Schories et al. 2003), and provides structure, shade, and transport for larval and juvenile fishes and decapods (Daniel and Robertson 1990, Wehrtmann and Dittel 1990, Schwamborn and Bonecker 1996).

Furthermore, the spring-neap alternation is correlated with the lunar phases and changes in moonlight intensity. Moonlight intensity can change the activity patterns of fish, but the effect is apparently negligible in turbid estuaries (e.g., Quinn and Koijs 1981, Krumme et al. 2004, Krumme et al. 2008) and more relevant on clear water coasts (Hobson 1965). Untangling the effect of moonlight and spring tide, however, is a formidable task due to statistical considerations. Lunar cycles only recur monthly. The need to sample several lunar cycles automatically adds the effects of month and/or season. In addition, tides can cause unexpected co-variation, e.g., consistently higher or lower tidal ranges at a certain lunar phase, so that the effects can be inextricably correlated.

8.7.3 Interaction Between Tide and Time of Day

Another particularity, absent from coasts with weak tides, is the fact that the diel and the tidal cycle act in concert and neither of the two factors can be studied without considering the other. Let us assume the most common case of a semidiurnal tide, and a neap high-tide occurring around 12:00 and 00:00 hrs. Due to the retardation from tide to tide a week later, at spring tide, high tides occur around 18:00 and 06:00 hrs. In-between, mid high-tides would occur around 15:00 and 03:00 hrs. Each of the six groups is characterized by a particular combination of light intensities, tidal heights, and current speeds. These unique combinations recur, however, on a weekly or fortnightly basis. Intertidal fish assemblages and penaeid shrimp (see Section 8.8.2) respond strongly to these interacting factors.

Laroche et al. (1997) and Krumme et al. (2004) found recurring fish assemblages following particular combinations between spring-neap tide and day-night. For a given site, the nektonic community is predictably reshuffled each tide. Given certain environmental conditions, mainly determined by the interplay of the diel (light intensity) and tidal cycles (water depth, current speeds), a specific assemblage temporarily colonizes the intertidal. The assemblages alter in a characteristic pattern that not only involves species presence or absence, but also proportional differences in the intertidal occurrence among dominant species. Consequently, results from one of these short-term combinations are not fully representative for the other combinations, and care should be taken against making premature conclusions when the full set of short-term assemblage combinations is not known. The variation caused by the interaction of the diel and tidal cycles can be equal to seasonal variations in tropical estuarine fish assemblages (Krumme et al. 2004). Therefore, long-term monitoring programs on (meso- and macro-) tidal coasts should seriously consider the short-term variation caused by the interactive effects of the diel and tidal cycles.

It is apparent that fishes do not use each tide to migrate and that considerable variation can occur between individuals (e.g., Szedlmayer and Able 1993), size groups (Bretsch and Allen 2006a), sexes (Krumme et al. 2004), species, and regions (Gibson 1973, van der Veer and Bergman 1987). Results from temperate coasts have shown that species such as the plaice *Pleuronectes platessa* change their migratory behavior during ontogeny (Gibson 1997). In juvenile plaice there are examples for each of the three high-tide distributional patterns for a population: (1) complete population shift to the intertidal (Kuipers 1973), (2) only partial spread (Edwards and Steele 1968, Ansell and Gibson 1990), or (3) separation in intertidal and subtidal fish populations at high tide (Berghahn 1987). The study of such variations can provide insight into the mechanisms controlling migrations.

8.8 Tidal Movements of Decapods

The responses of decapods to tidal currents vary from avoidance of displacement, to intermittently walking and swimming, and selective tidal stream transport (Forward and Tankersley 2001). Connectivity by short-term movements between adjacent tropical ecosystems is most evident in the intertidal migrations of penaeid shrimps and swimming crabs.

8.8.1 Lobsters

Settled lobsters are not adapted to swim in tidal currents. The tides rather confine than foster the activity and movements of lobsters. Their natural behavior enables them to live on coasts with high tidal velocities. They shelter in areas of reduced flow on the sea bed or bury themselves in soft sediment. Instead of using the tide to move, lobsters have to reduce their mobility during stronger current periods to avoid displacement (Howard and Nunny 1983). In fact, lobsters of British coastal water approached baits only during the period of slack water (Howard 1980).

8.8.2 Penaeid Shrimps

Shallow, tidally influenced, and often turbid waters commonly provide essential nursery grounds for many commercially important penaeid shrimps. Juvenile penaeid shrimps are frequent visitors in intertidal mangroves at high tide (e.g., Staples and Vance 1979, Robertson and Duke 1987, Chong et al. 1990, Vance et al. 1990, Mohan et al. 1995, Primavera 1998, Rönnbäck et al. 1999, Krumme et al. 2004), as well as mudflats (e.g., Bishop and Khan 1999) and seagrass beds (Schaffmeister et al. 2006). On short-term migrations within the nursery ground the shrimps regularly transfer energy from the littoral to the sublittoral. Ontogenetic movements as part of their life cycle export the accumulated energy to the coastal ocean via reproductive offshore migrations (see Chapters 4 and 7). Kneib (1997) described this successive and stepwise export of energy via tidal and ontogenetic movements of fish and decapods in saltmarshes and aptly named it a ‘trophic relay’.

Catchability of juvenile shrimps by trawls is often highly variable in space and time. The availability of shrimps depends on the species, behavior (i.e., buried or not, active or not), and response to the sampling gear (Vance and Staples 1992). Shrimp species such as *Penaeus merguiensis* are most active during nightly high tides (Dall et al. 1990), but are most catchable by trawls at low tides (e.g., Vance and Staples 1992). Other species such as *P. semisulcatus* and *P. esculentus* are more catchable during nightly high tides.

On a short-term scale the migratory behavior of shrimps closely responds to the interactive effects of the diel and tidal cycles as shown both in the field (Staples and Vance 1979, Vance and Staples 1992) and in laboratory experiments (e.g., Hindley 1975, Natajaran 1989a, b, Vance 1992). The relative strength of the response to the tide and light cycle is species-specific (Vance and Staples 1992). The interaction of these factors can lead to confounding effects that make the establishment of standard sampling programs difficult (Staples and Vance 1979, Bishop and Khan 1999). Laboratory studies further suggest that the activity of shrimps may change with turbidity, moonlight, salinity, and temperature. Figure 8.9 illustrates the complex

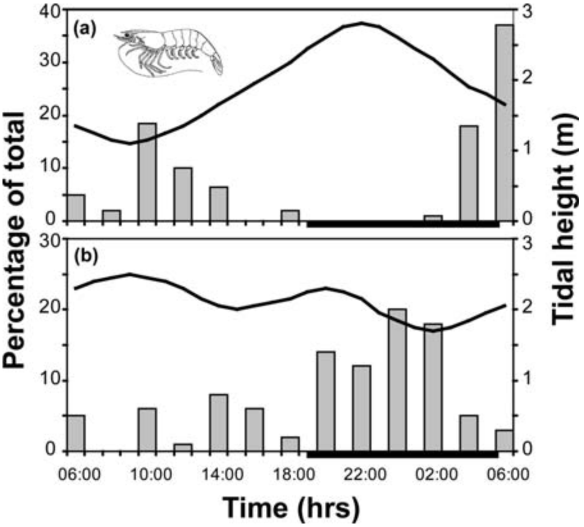

Fig. 8.9 Effect of the tidal (solid lines) and diel cycles during (**a**) a diurnal spring tide ($N = 529$), and (**b**) a semidiurnal neap tide ($N = 638$), on catchability (vertical bars) of juvenile *Penaeus merguiensis* in the Embly River, Gulf of Carpentaria, tropical Australia. Black horizontal bars on X-axes indicate hours of darkness. Modified after Staples and Vance (1979), with kind permission of DJ Vance. Reproduced with permission from the Australian J Mar Freshw Res 30(4):511–519. Copyright CSIRO (1979). Published by CSIRO PUBLISHING, Melbourne, Australia

interaction of the tidal and the diel cycles and, in particular, the influence of different tidal types on the catchability of *Penaeus merguiensis* near Weipa, eastern Gulf of Carpentaria, Australia. The tidal stage was more important than the time of day as suggested by a unimodal distribution during a diurnal tide and a bimodal distribution in catches at a semidiurnal tide.

Similar to many tidally migrating fish, there is information on the end points of the migration, i.e., the resting and feeding sites, but information on the movements connecting the end points is scarce. Some shrimp species such as *Penaeus merguiensis* are known to congregate in shallow water during the low-tide period, often close to the water edge (e.g., Hindley 1975, Hill 1985, Vance et al. 1990). Others such as the tiger prawn *P. monodon* bury and do not congregate near the water's edge. The smallest juvenile shrimps often inhabit more shallow water and the larger individuals live at greater depths (e.g., Staples and Vance 1979). With the flood tide the shrimps move upstream and enter intertidal mangrove-lined creeks.

Inundated mangroves provide a number of microhabitats for shrimps, but the high-tide distribution of shrimps in mangroves is highly variable (e.g., Rönnbäck et al. 1999, Vance et al. 2002, Meager et al. 2003). Factors such as local currents, topography, habitat type, and site-specific water clarity as determined by water depth and turbidity may play a role in influencing the distribution of shrimps in these intertidal microhabitats. Quinn and Koijs (1987) and Vance et al. (2002) have suggested that the movements of the shrimps are strongly influenced by the local currents. Krumme et al. (2004) found a significant positive relationship between the high-tide level and the abundance and catch weight of *Penaeus subtilis* from intertidal mangrove creeks. Depending on the local topography, tidal movements can take shrimps as far as 200 m into the mangrove forests (Vance et al. 1996, Rönnbäck et al. 1999, Vance et al. 2002). Feeding seems to occur mainly during high tide (e.g., Robertson 1988). Vance et al. (1990) suggested that at ebb tide the shrimps move downstream by both active and passive movements. They may, however, control downstream displacement at ebb tide by near-bottom activity, and return to the subtidal at very low intertidal water levels and concentrate along the turbid water edge during low tide, from where they may or may not enter with the next flood tide.

Little is known about differences or changes in the proportions of tidally migrating shrimps in a population. Bishop and Khan (1999) distinguished between subtidal and intertidal mudflat shrimps. Subtidal shrimps are unlikely to regularly connect adjacent ecosystems. Schaffmeister et al. (2006) caught juvenile and subadult *Palaemon elegans* from seagrass ponds at low tide in Mauritania and marked them with bright nail polish. Sample size and the recapture rates were low but the results suggested that juveniles left the ponds at flood tide to forage in the surrounding seagrass, and that some returned to the previously occupied pond while others were found in adjacent ponds at low tide. Subadults remained in their home pond at high and low tide. A better understanding of the fine-scale intertidal movements of decapods requires localized studies following the movements of individual shrimps while migrating with the tides.

8.8.3 Portunid Crabs

Tidal movements are likely common in tropical swimming crabs, but surprisingly little information has been published. Important parameters that determine migratory activity are age, sex, and molting stage. Hill et al. (1982) found that juvenile mud crab *Scylla serrata* were resident in the intertidal mangrove zone, similar to juvenile *Portunus pelagicus* that remained in intertidal pools at low tide (Williams 1982). The majority of subadult and on occasion adult mud crabs moved in the intertidal zone only during high tides and retreated to the subtidal zone at low tide (Hill et al. 1982). Sublittoral estuarine adult *S. serrata* ‘live a free-ranging non-territorial existence’ (Hill 1978). They may stay in the same area (<1 km) for longer periods or move larger distances downstream (>10 km) within weeks. Hill et al. (1982) suggested that reduction of intraspecific competition and feeding are the main reasons for intertidal migrations of *S. serrata* and the intertidal residence of juveniles, thus indicating that tidal migrations possibly serve as a means of avoiding intraspecific competition (see Section 8.6.3).

Regular movements to and from the intertidal with the rising and falling tide, respectively, have been reported for *Thalamita crenata* (Cannicci et al. 1996), *Callinectes sapidus* (Nishimoto and Herrnkind 1978), *Cancer magister* (Williams 1979), and *Carcinus maenas* (Dare and Edwards 1981). *T. crenata* showed greatest activity when the intertidal water level was between 10 and 40 cm high (Vezzosi et al. 1995), and used landmarks to locate its refuges and was able to home (Vannini and Cannicci 1995, Cannicci et al. 2000).

On temperate tidal coasts, juvenile blue crabs *Callinectes sapidus* enter the intertidal zone with the flood tide but usually do not venture far into the saltmarsh (<100 m; Fitz and Wiegert 1991, Kneib 1995). At low tide they may bury in shallow water (van Montfrans et al. 1991). *C. sapidus* stomachs were fullest at high tide, indicating that the immigration during flood tide is used as an active feeding period (Ryer 1987). Thus, the tidal cycle may result in cycles of food intake in the blue crab (Weissburg and Zimmer-Faust 1993, 1994, Zimmer-Faust et al. 1995, 1996, Weissburg et al. 2003). Cannicci et al. (1996) reported greater feeding of *Thalamita crenata* at spring than at neap tides.

8.9 Comparison of the Degree of Habitat Connectivity among Geographic Regions

The available literature suggests that heterogeneous seascapes are often tightly connected by short-term, i.e., diel and tidal movements of nektonic organisms (for population connectivity due to ontogenetic migrations refer to Chapters 6, 7, 10). The degree of connectivity among habitats may, however, differ between regions.

One important factor for regional differences in short-term habitat connectivity is hydrology. The tidal ranges in the Indo-West Pacific are generally greater than in the Caribbean, which may facilitate connections between adjacent ecosystems. Short-term movements need not be restricted to the diel cycle, i.e., there is only one round trip in 24 hrs. On coasts with semidiurnal tides, two round trips in 24 hrs are possible; as a consequence, subtidal habitats can house both diel and tidal visitors. Evidence for diel and tidal habitat connectivity in the Indo-West Pacific either originates from just one habitat (seagrass) and only infers connectivity to adjacent habitats (e.g., Kochzius 1999, Unsworth et al. 2007a) or is in fact based on results from several adjacent habitats (Nakamura and Sano 2004, Dorenbosch et al. 2005, Unsworth et al. 2007b, Unsworth et al. 2008).

Due to the negligible tidal pulse, twilight movements are the major driver of short-term habitat linkages in the Caribbean. The link between Caribbean mangroves and seagrass and reef fish fauna may be relatively strong because the latter two habitats can occur sufficiently close to mangroves to allow diel fish connectivity. However, on a global scale, the Caribbean mangroves are an exception rather than the rule. Unlike most other tropical mangrove coasts of the world, the Caribbean patch mangroves thrive in this clear-water environment with relatively little terrestrial runoff, are continuously inundated, and thus are always accessible to nektonic organisms. Commonly, mangroves and muddy mangrove-lined channels and creeks are intertidal, and access is restricted to periods of inundation.

Another factor is species richness and the composition of functional groups. In the Indo-West Pacific, more species are potentially involved in short-term interhabitat migrations. All functional fish groups have more species here than in the

Caribbean (Bellwood et al. 2004). Particularly, invertebrate feeders, and diurnal and nocturnal planktivores are more diverse in the West Pacific. Haemulidae are the dominant diel migrants of Caribbean reefs and are more diverse here than in the Indo-West Pacific. However, there are several other families whose inter-habitat connectivity has been demonstrated (Table 8.1) that have greater species richness in the Great Barrier Reef (Bellwood and Wainwright 2006), e.g., Pomacentridae, Apogonidae, Holocentridae, Lutjanidae, Mullidae, and Siganidae. Apogonidae are the dominant nocturnal planktivores of the Indo-Pacific reefs, both in terms of abundance and species diversity. Parrish (1989) suggested the connecting function of Caribbean Haemulidae may be substituted by Lethrinidae, though this family is less dominant in the Indo-Pacific than Haemulidae in the Caribbean. More qualitative and quantitative field evidence of short-term inter-habitat linkages is needed for the majority of the families listed in Table 8.1. The Indo-West Pacific in particular is lacking in this kind of data.

8.10 Tidal Range and Home Range Size

Pittman and MacAlpine (2003) suggested that there is unlikely to be a strong linear relationship between fish body size and home range size due to geographical and high intra- and interspecific variability in fish behavior. Large reefal top predators can be both highly mobile (Meyer et al. 2007a, b) or extremely sedentary (Zeller 1997, Kaunda-Arara and Rose 2004, Popple and Hunte 2005). Tiny fish can occupy territories extremely small in size, yet migrate vast distances to find plankton patches, such as anchovies. Thus, habitat connectivity due to migration is not a simple function of fish size.

Habitat connectivity is likely greatest where multiple habitat types are coexisting in close proximity. Yet, when profitable habitats are more distant, increased tidal ranges, i.e., higher current speeds, may facilitate traveling to otherwise remote resources and shelter sites. It is postulated here that the home range size of the same or cognate species is greater when the tidal range and currents are greater and that therefore, habitat connectivity by short-term movements is likely greater than on coasts with negligible tides.

Two examples illustrate the potential increase in home range size due to increased tidal range. In Trinidad, where the tidal range is ~0.5 m (Wothke and Greven 1998), the four-eyed fish *Anableps anableps* occupies a home range with a maximum distance of <100 m (H Greven, University of Duesseldorf, Germany, pers. comm.). In north Brazilian mangrove creeks, where the spring tide range is between 3 and >4 m, the same species may travel >1.5 km between low-water resting and high-water feeding sites each tide, i.e., >3 km per day (U Krumme, unpubl. data). Likewise, the ariid catfish *Sciades herzbergii* may occupy home ranges <1 km in the southern Caribbean (A Acero Pizarro, INVEMAR, Colombia, pers. comm.) where tidal ranges are ~1 m, whereas the tidal movements of the same species in north Brazil may also cover distances >1.5 km per tide (U Krumme, pers. observ.). It should be noted, however, that the increase in home range size in the two examples by more than one order of magnitude between a micro- and macrotidal area is also due to differences in topography between the two sites. The larger the tidal range and the flatter the intertidal, the greater the possible distance of intertidal upshore excursions and the greater the home range occupied by a population of transients. In the case of subtidal migrations, increased foraging ranges would largely be a result of greater current speeds that allow for greater distances covered each tide.

Where different ecosystems co-occur, a much greater proportion of the heterogeneous ecosystem is accessible to nektonic organisms when current speeds are increased. When a greater tidal range increases foraging range, use of more distant sites becomes profitable and habitat connectivity increases. Alternatively, nektonic species at macrotidal coasts may simply undertake longer migrations to a similar number of sites that are, however, more profitable than the restricted number of sites accessible in a microtidal setting. Accessibility of more profitable sites should result in faster growth, reduced mortality, and greater recruitment of juveniles to the adult stock. If 'the greater the tidal range, the greater a species home range' holds true, it is evident that marine parks on macrotidal coasts need to be much larger than those on microtidal coasts.

8.11 Tides—an Overlooked Component of Variation Between Coasts

The diversity of tidal pulses – as briefly outlined in Section 8.3 – is a component of variation between coasts that seems to be fairly overlooked in large scale comparisons of biodiversity or productivity among coastal regions. Tides are the principal pulse for exchange processes linking adjacent coastal ecosystems on the short- to medium-term, and are the key engineers of coastal processes that determine ecosystem productivity and functioning in the long term. Tides regularly expose the intertidal which is particularly rich in epifauna and flora and provides the nursery grounds for various marine species. Tides create currents that mix the sediment and resuspend nutrients that enhance plankton production, fostering the production of higher trophic levels. Tides transport plankton to sessile filter feeders that provide food and shelter to other organisms.

Clearly, tides add a significant level of natural disturbance to a coastal system. Systems under different regimes likely have different natural levels of habitat connectivity, vulnerability, and resilience against disturbance. According to the intermediate disturbance hypothesis (Connell 1978), which proposes that the highest diversity is maintained at intermediate levels of disturbance, meso- or macrotides may favor a greater habitat connectivity and resilience, and a lower level of vulnerability of coastal ecosystems. (i) In systems with weak tides such as the Caribbean, short-term exchange processes are restricted to ocean currents and active animal movements related to light intensity. A given set of species lives under these conditions and exhibits a certain level of habitat connectivity between the coastal systems. Local disturbances are barely buffered by adjacencies. (ii) In intermediate tide systems, life is more dynamic. Exchange processes are facilitated by the tide (e.g., for filter feeders and higher trophic levels). Habitat connectivity is increased by tidal movements. Disturbances can be buffered from adjacent areas. Species benefit from the increased movement of the water. (iii) In systems with strong tides, life is very dynamic and habitat connectivity may be high. However, certain species may be excluded (e.g., frequent sediment rearrangement excludes long-lived sessile organisms). Disturbances have to be high to add to the naturally high level of disturbance of a system with macrotides.

It is reasonable to assume that tidal range and tidal type influence species diversity and ecosystem functioning. Besides biogeographical differences in species richness and composition of functional groups in the Indo-Pacific coasts (see, e.g., Bellwood et al. 2004), intermediate tides may favor greater habitat connectivity and resilience, and a lower level of vulnerability in Indo-Pacific coastal ecosystems compared to the Caribbean. Unsworth et al. (2007b) noticed considerable variation between the seagrass fish fauna in Indonesia and other Indo-West Pacific regions which might be due to different tidal regimes.

Given that the tidal ranges on the Caribbean coasts are very small, biological studies comparing the Caribbean and the Indo-West Pacific are only appropriate when areas with weak tides of similar seascape configuration are compared. Consequently, due to a tidal range >3 m in the Great Barrier Reef, comparisons with the Caribbean are inherently faulty because they compare two systems with different levels of natural disturbance. Consequently, to reduce the likely variation between data sets and thereby increase our understanding of the variation caused by different tidal regimes, future studies should (1) compare systems in different geographical regions but of similar tidal regimes (e.g., coasts with weak tides in the Caribbean vs. coasts with weak tides in the Indo-West Pacific), or (2) compare systems from similar geographical regions, i.e., with similar species communities, but of different tidal regimes (e.g., Caribbean vs. Brazilian coast, numerous study comparisons would be possible in the Indo-West Pacific region). In Recife, East Brazil, fishermen report that different age groups of different species move between specific sites in a mangrove/seagrass/coral reef seascape according to the interactive combination of tide and time of day (S Schwamborn, Universidade do Estado da Bahia, Brazil, pers. comm.). This results in more complex patterns of habitat connectivity in heterogeneous seascapes exposed to meso- and macrotides than in microtidal areas such as the Caribbean.

Several hypotheses remain untested. Are there overall differences in life history patterns (migrations, growth performance, or natural morality) within a species from similar micro-, meso-, and macrotidal coasts? Do different tidal regimes lead to detectable differences in the functioning of ecosystems?

If tidal range and the functioning of ecosystems in fact significantly interact, the scope of broad-scale comparisons must be redefined with a new focus on variation caused by differences in tidal regimes. There is certainly a need for enhanced international cooperation which should include multi-national projects, with standardized methods and sample designs to allow comparisons between results, in the search for global patterns and improved conservation of tropical marine resources.

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