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1 Sensory biology and navigation behavior of reef fish larvae

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Spurred by the still accelerating progress made in the last decade(s) in our knowledge of the behavioral capabilities of coral reef fish larvae, we review their sensory world and its potential for orientation and homing navigation. We now know that these millimeter-sized animals have swimming and sensing capabilities that could influence their advective dispersal. During the pelagic phase, sustained swimming capabilities increase to speeds exceeding prevailing currents and senses develop that could steer them. After hatching, the nose develops from bilateral sensory patches to an active odor-sampling organ that recognizes habitat and social odors, some apparently learned at the hatching stage. As larvae grow, vision improves from light detection to image formation: the eye and lens grow proportionally and the retina becomes steadily more organized resulting in greater acuity and possibly allowing UV and polarized light detection. Growth of the vestibular apparatus, including the otoliths, should enhance hearing, while a swim bladder, present in some species even prior to hatching, should further increase hearing sensitivity and higher frequency detection. The brain shows its major subdivisions well before hatching and continues to grow rapidly. Behavioral experiments suggest that this brain can extract and store environmental information that can be used in orientation, navigation, and settlement. Here, we discuss the ontogeny of swimming behavior and the multi-sensory control that may be involved in orientation and navigation. The evidence is based on anatomical and behavioral studies of larvae and on the physical dispersal patterns and detection distances of sensory stimuli. However, obtaining pelagic-phase experimental data from these widely dispersed, "invisible" propagules is exceedingly difficult. We emphasize the essential role of learning and present a behavioral hypothesis of homing navigation. Much remains to be learned to improve the accuracy of dispersal models in capturing larval behavior and predicting recruitment patterns needed for management of sustainable populations and their habitat in a time of global change.

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This chapter reviews the sensory biology of coral reef fish larvae and explores the mechanisms involved in their active participation in dispersal and recruitment processes. Pelagic larvae are exposed to the locally prevailing ocean currents for several weeks and face the risk of long-distance transport from which return to a settlement reef is possible only through sustained, goal-directed swimming. While it is likely that many will die [119], that same probability also suggests selection for behavior that can diminish this threat. The evolutionary response would be the emergence of behavior that promotes retention near the reef and mechanisms to return to the reef environment if local retention fails. Such capability would suggest that early larvae might imprint on local sensory cues and use them during subsequent larval stages for retention and homing navigation.

The term “navigation” is used in many different contexts. For this chapter, we adopt a broad concept of navigation as “goal-directed movement through a landscape”, including the use of maps and compasses. For larval reef fishes this would be sustained swimming across a map of recognizable features (odor, sound) to remain or arrive at the home reef or any suitable reef. We certainly do not imply here that larvae use what is known as “true navigation” defined as a map sense where the animal knows both its own position and the goal position, and can compensate for displacements to reach the goal from any angle. Particularly in early stages of research it is important to observe the phenomenon without prejudice and without the confining terms of narrow definitions. An illuminating introduction is given in *Nature’s Compass* [955], an in-depth review in *Spatial Orientation* [2283].

The null model of treating coral reef fish larvae as passive particles, at the mercy of ocean currents, started changing in the 1990s (see [1467]) with field and lab studies showing higher than expected levels of self-recruitment [1289,1297], considerable swimming capabilities [1446,2434], and behavioral responses to odor [92,101,1920] and sound [2361,2507]. The common practice of using light traps provides evidence of responses to light. Anatomical studies show that all the major senses are present at hatching, albeit in still rudimentary shape. All this evidence points to a plausible new model that larvae may be able to influence their dispersal by reducing the probability of losing direct sensory contact with the reef and to return to the reef from greater distances. Both retention in leeside eddies and returning from greater distances would be enhanced by appropriate behavior and reduce the lethal threat of drifting beyond a range from where settlement is possible.

To counter this lethal threat the larvae must know the “home” direction and be able to swim directionally for the duration required to find a settlement reef. The most likely reef they can “know” is the birth reef and the most likely cues are the odors and sounds that identify reefs. If they were to imprint on either or both cues they could use this map information to remain within

sensory contact with the reef and enhance local retention. Those who do not stay within the reef halo of odor and/or sound would need to know their drift direction and swim in opposite direction to return to the reef area. As measuring drift is not trivial when fixed visual cues are absent, it is more likely that the larvae use a compass. Prevailing self-recruitment suggests that local populations are resident in the same geographic area, for instance at remote reefs; this could have led to an innate compass direction based on predictable currents. Plausible as it may sound, we still know very little about larval navigation. This chapter explores both the physical probability and biological potential for navigation of larval reef fishes.

To properly describe the plausibility of such a broad scenario it is important to describe (1) the physics of the sensory stimuli potentially available to the larvae, (2) the swimming capabilities and the sensory anatomy and physiology of the developing larvae, and (3) the behavioral evidence for navigation. The sensory sections are organized accordingly for each of the major senses. Each section starts with “physical constraints”, indicating both the potential for and limitations of the stimulus for orientation and navigation. As the basic physics is textbook material, it is not specifically referenced. This is followed by sensory anatomy/physiology and behavior. In all behavior, learning and memory play critical roles. Thus the sensory sections are followed by a brief section indicating how little we know about learning in reef fish larvae. Finally, the section on navigation presents evidence for sensory maps and compass orientation, ending with an example.

A caveat is that in a single chapter only the most pertinent aspects of the stimulus world can be indicated. The interface between physics (oceanography and sensory stimuli) and biology (sense organs and behavior) provides a fruitful terrain for discovery of processes that drive larval dispersal and recruitment and, over a longer time scale, the distribution of species. We hope that this chapter will stimulate interest in the physics of the marine environment, which has forever both spurred and constrained the evolution of swimming and sensory capabilities, i.e. the larval umwelt.

SWIMMING CAPABILITIES

Initially, after hatching, larvae are plankton operating in a viscous medium (Reynolds number $Re = 40$) with limited capability for sustained swimming. As they grow, they soon become nekton and swimming becomes “inertial” ($Re = 4000$) [1457]. *In situ* observations by divers and laboratory tests in small flumes have shown the ontogeny of remarkable speed and endurance. Forced swimming tests in flumes give an important impression of capabilities, but may not be what larvae actually do over sustained time periods in the field, where drifting may be an important part of their pelagic existence [1148].

In situ observations

In a size range of 7–55 mm, swimming speeds observed *in situ* in 50 different species ranged from 2 to 65 cm s⁻¹, generally correlated with size and often faster than ambient currents. From this remarkable early study, the authors concluded correctly that this capability could both enhance and limit dispersal [1446]. Another pioneering study of *in situ* larval swimming showed that settling-stage coral trout (*Plectropomus leopardus*) moved faster in open water or when directed away from a reef (~18 cm s⁻¹) than over and toward a reef (~7 cm s⁻¹) with the large majority swimming directionally at variable depths and directions [1448]. These studies were the first to document directional swimming in the field, limited to the 10-minute period typical for diver observations. Swimming directionality over a 20-minute period was demonstrated in a drifting observation chamber [1920] showing that pelagic reef fish larvae discriminated reef odor and responded by changing their swimming speed and direction.

Flume tests

Controlled swimming-endurance tests in flumes showed results for swimming speeds comparable to *in situ* measurements and allowed analysis of several factors influencing swimming behavior capabilities [2434]; and many other studies followed. Bellwood and Fisher [192] came to the remarkable conclusion that at speeds of 49 body lengths/s larvae of anemone fishes (7 mm TL, total length) “approach the maximum limit for sustained aquatic vertebrate locomotion”. Calculations based on swimming speeds of zero at hatching and a species-specific maximum at settlement show that most reef fish larvae would be able to modify their advective dispersal (i.e. drift in currents) for the greater part of their pelagic phase [820]. Body size and propulsive area were found to be predictive for swimming speed in late-stage larvae of many species, so that these anatomical features may be useful to predict swimming speeds [821]. As expected from hydrodynamic and metabolic considerations, maximum speed is inversely correlated with endurance; the latter presumably leading to greater distance covered in the field [818]. In addition, starvation had a long-term negative effect on swimming endurance, although not over a period of a few days [791]. Video analysis under less constricted laboratory conditions showed that pomacentrid and apogonid larvae swam more at night, particularly during the later pelagic period [819]. After settlement, swimming speeds can decline quickly and drastically: 50% in 2 days [1463]. Leis [1462] provides an extensive review of the ontogeny of behavior in larvae of marine demersal fishes and concluded that their passive (planktonic) stage is short, followed by a nekton stage of considerable swimming power and sensory capabilities. Of course, fish larvae can adjust their vertical position in the water column upon hatching and already influence their dispersal without significant swimming [1918].

SENSORY CAPABILITIES

The initially unexpected larval mobility, speed, endurance and directionality have the potential to be used for navigation that could significantly alter dispersal and settlement: fish larvae could use it to enhance or limit their dispersal by advection or maintain their position relative to a reef. Of course, navigation depends prominently on the use of sensory information.

Olfaction: a sense organ to analyse ambient odors

The neuro-anatomy and behavioral function of the two major chemical senses, olfaction and taste, are radically different, although some chemical compounds such as amino acids can be smelled and tasted [100]. In all vertebrates, olfaction is mediated by olfactory neurons projecting to an olfactory bulb and olfactory tract (cranial nerve I, often called the olfactory nerve) entering the forebrain. Its function is monitoring ambient chemical signals. In contrast, the sense of taste is mediated by epidermal cells forming taste buds, which are innervated by the facial and glossopharyngeal/vagal cranial nerves (VII and IX/X, respectively) entering the dorsal hindbrain in two distinct facial and vagal lobes. “Facial” taste predominates on lips, barbels, and in some fish (e.g. catfishes) entire body surfaces; it serves in food recognition and triggers the “pick-up” reflex. Vagal/glossopharyngeal taste occupies the mouth, gill arches, and pharynx where it checks food and triggers the swallow reflex [99]. In addition, some fish have solitary chemoreceptor cells that respond to social odors [1951]. In sum, taste is typically used for local food quality assessment at very close range and only in rare cases for tracking (food) odor plumes (e.g. catfishes [99]). Here, we focus on olfaction and its use in recognizing ambient odors in a wide range of contexts, including food, predation, and social cues. Odors are non-directional and disperse with currents. It follows that fish use their lateral line and also vision to track currents that are identified by odor as being important (see below).

Physical constraints of odor Odors are perceived chemical cues; in water, they are dissolved or suspended. Their enormous variety makes them uniquely suited to distinguish subtle odor patterns, casually known as “bouquets”. Each individual fish and each reef has its unique bouquet. However, odors are non-directional and their turbulent dispersal makes odor concentration gradients – which are directional in theory – rarely useful to animal orientation, particularly in very small animals. Thus, olfaction can be used to identify odor sources and to keep animals motivated to search for them while other senses, lateral line and vision, are used to direct the search [903,905]. The fluid dynamics of odor dispersal in water, nasal flow regulation, and odor plume tracking behavior have been reviewed recently [102]. It is important to recognize that both reef odor and particles, such as fish

eggs and larvae, disperse simultaneously with their local current regime. Currents that are relevant to this chapter can be roughly classified into three categories. Reversing tidal currents are predictable on a daily scale and move odor and particles back and forth along and across reefs forming alternating leeside eddies in both directions. Tidal reversals can be, but do not need to be, symmetrical; these currents both disperse and retain odor and particles, creating odor “halos” around each reef. Persistent unidirectional “drift” currents, such as trade-wind-driven surface currents, are seasonally predictable and disperse odor and particles away from the reef of origin while retaining some fraction in a single leeside area. Mesoscale eddies and decadal currents are more difficult to predict and move entire regional current systems with potential for long-distance dispersal [102]. It is unlikely that larvae can monitor their drift.

Anatomy and physiology The fish olfactory system consists of neural elements (receptor neurons and olfactory bulb) and peripheral structures (ventilation mechanisms that regulate efficient water flow across the epithelium). Embryologically, an olfactory placode with receptor neurons develops as a patch in front of the eyes (Figure 1.1). As this epithelium grows it becomes folded into lamellae after sinking into a sac from where several structures emerge that drive the water/odor across the epithelium with a velocity that optimizes time for odor diffusion to the olfactory receptors. A larger outflow naris located higher on the skull, sometimes with a skin flap acting as a foil, generates suction when swimming or facing a current, while an inflow naris can become elongated with a small tube to facilitate access to water/odor flow outside the fish’ boundary layer (see Figure 1 in Lara [1420]). Via a soft membrane, breathing-related pressure changes in the buccal cavity can drive pulses of water through the olfactory sac: i.e. the fish “sniffs” with every breath. At settlement, cardinal fish larvae, *Ostorhinchus doederleini*, have three lamellae, and a fully developed, sniffing nose [101], similar to the coral-dwelling goby *Paragobiodon xanthosomus* [94]. Other species or earlier developmental stages have motile cilia driving water over the nose. Lara [1420] provides the most extensive analysis and review of larval and post-larval olfactory anatomy in 14 reef fish species. Anatomical development – quite variable for different species – predicts that larvae from hatching to settling continuously improve their ability to obtain and analyse odor samples. More lamellae support more receptor cells, thus predicting lower detection thresholds and a wider odor spectrum. Two bilateral nostrils might be used for aspects of steering in odor plumes [904]. One can thus use anatomy to estimate olfactory capabilities.

Physiological experiments on larval reef fish olfaction are challenging, but Wright *et al.* [2739] succeeded in recording electrical brain activity in settlement-stage *Pomacentrus nagasakiensis* in response to conspecific odor and the amino acid L-alanine. The fact that both a food and social odor evoked

brain responses might suggest that the larvae could have both a main olfactory sense (for food detection) and an accessory olfactory (“vomeronasal”) sense for social recognition as seen in other fishes [1029].

Odor preference Evidence for the possible role of odor in larval navigation has come primarily from odor choice experiments in a (field-) laboratory setting using near- and post-settlement-stage larvae freshly captured from light traps and crest nets. Odor preference could suggest a navigational role of odor by providing broad landmark information (see below).

Anemone fish, *Amphiprion melanopus*, recognize host anemones by olfaction, not vision [92]; they show a life-long olfactory preference for their obligate anemone host. Some species are highly specific, others accept different anemone hosts [93]. In addition to local host odors, recently settled *Amphiprion percula* and several other species can use large-scale habitat odors: in two-channel odor choice flumes they showed strong preference for water treated with leaves that are characteristic for reefs around forested islands [675,677]. Similarly, pre-settlement apogonid and pomacentrid larvae preferred reef/lagoon water to ocean water [101] and the odor of their capture reefs to odors from several other nearby reefs [929]. The latter result demonstrates that even close reefs can have different odors. *Ostorhinchus doederleini* larvae did not change their odor preference for the capture reef even after living for several days in water from a nearby reef, showing that odor preference was not based on habituation to more recent odors and suggesting early odor imprinting [1708]. Newly settled juveniles of three common coral-associated species in Kimbe Bay, Papua New Guinea, chose the odor of conspecifics and live coral over water without reef cues and strongly avoided the odor of degraded coral [556]. Some species in French Polynesia chose coral to algal odor, again with implications for reef degradation [1438]. Post-larvae of the coral reef fish *Haemulon flavolineatum*, which initially settle at mangroves and seagrass beds, prefer their odor to coral reef odor [1200]. They can also use visual, acoustic and hydrodynamic cues; in odor preference tests, the simultaneous visual presence of conspecifics took precedence over odor [1200]. In choice tests, larval preference for conspecific odor was more common than for habitat odor [1433,1437]. *Chromis viridis* larvae responded positively to visual, “acoustic/vibratory”, and olfactory cues from conspecifics but not heterospecifics or coral substrates [1433]. In *A. percula* and *A. melanopus* preference for habitat odor switched from avoidance to attraction one week after hatching apparently serving first dispersal and then recruitment [677].

In general, the function of odor appears to be its – often learned – association with important environmental features, including large- and small-scale habitat and its conspecific and heterospecific inhabitants. For navigation, this information can serve as a regional map of various odors. However, the presence of

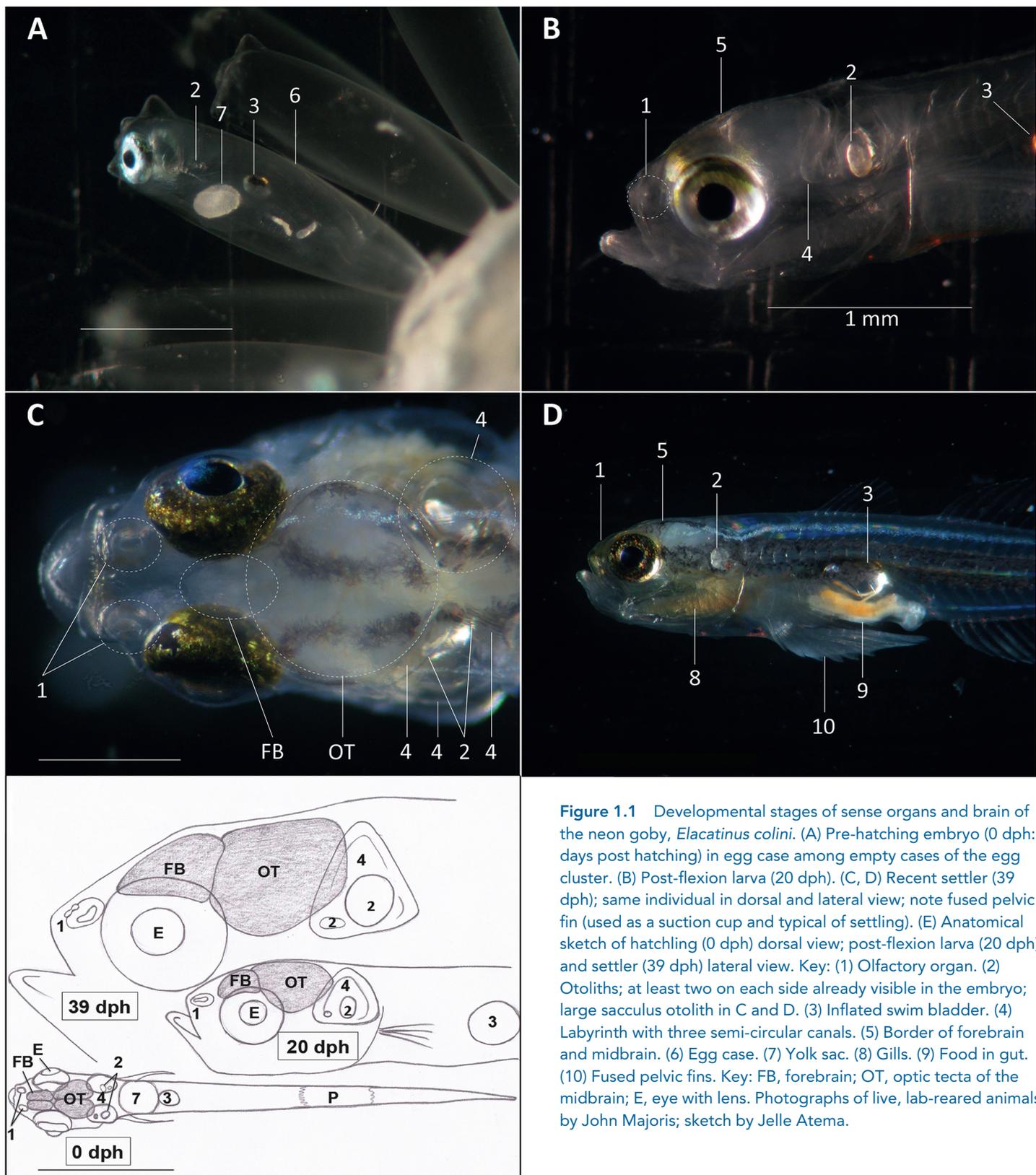


Figure 1.1 Developmental stages of sense organs and brain of the neon goby, *Elacatinus colini*. (A) Pre-hatching embryo (0 dph: days post hatching) in egg case among empty cases of the egg cluster. (B) Post-flexion larva (20 dph). (C, D) Recent settler (39 dph); same individual in dorsal and lateral view; note fused pelvic fin (used as a suction cup and typical of settling). (E) Anatomical sketch of hatchling (0 dph) dorsal view; post-flexion larva (20 dph) and settler (39 dph) lateral view. Key: (1) Olfactory organ. (2) Otoliths; at least two on each side already visible in the embryo; large sacculus otolith in C and D. (3) Inflated swim bladder. (4) Labyrinth with three semi-circular canals. (5) Border of forebrain and midbrain. (6) Egg case. (7) Yolk sac. (8) Gills. (9) Food in gut. (10) Fused pelvic fins. Key: FB, forebrain; OT, optic tecta of the midbrain; E, eye with lens. Photographs of live, lab-reared animals by John Majoris; sketch by Jelle Atema.

an olfactory epithelium at hatching does not demonstrate that a larva can smell; smelling involves brain processing. More detailed analysis of olfactory physiology and genetics is needed and may reveal receptors tuned to important odors, including reef-identifying chemicals. Lecchini *et al.* [1434] initiated chemical – chromatographic – analysis of reef odors. Of course, most natural behavior is based on multi-sensory information. The best use of odor is for identification of important targets and conditions such as food, conspecifics, and reef halos, which might serve as maps.

Hearing

Hearing in fish is different from human hearing due to the density of water, which results in (1) $\sim 5\times$ greater propagation speed and (2) virtual sound transparency of many fish bodies which are nearly as dense as the water. In addition, (3) fish ears are not widely separated and (4) the swim bladder (when present) re-radiates sound from within the body to the ears. These four factors have important consequences for sound localization. Sound is an audible propagated pressure wave. The audible frequency range for humans is typically given as 20–20 000 Hz; for fish it greatly depends on species but best frequencies are often reported between 20–200 Hz. Sound detection in fish involves multiple motion detecting organs, all based on directionally polarized “haircells”: the acoustico-lateralis system. Hearing in fish involves the otolith, lateral line, and swim bladder organs. Later we address turbulent advective flow patterns and hydrostatic pressure; their detection could overlap with hearing.

Physical constraints Sound sources generate both propagated pressure waves and more local hydrodynamic flow patterns; the two attenuate differentially with distance [1305]. As pressure and particle motion are inextricably connected, sound can be measured with pressure and/or motion detectors. Theoretically, the linear decay of particle motion associated with pressure wave amplitude intersects with the exponential decay of hydrodynamic wave amplitude at a distance of about a sixth of the wavelength, e.g. 2.5 m away from a 100 Hz source. This is considered the boundary of an acoustic nearfield and farfield. The nearfield contains better hydrodynamic (i.e. “flow”) and directional information, while the farfield ranges much further but is still poorly understood in terms of direction detection by fish.

Idealized – i.e. unbounded – conditions assumed for this computational model (e.g. Kalmijn [1305]) are usually not met in nature where dispersal fields are more complex [2162]. The sound nearfield is not directly source oriented and can be detected with motion sensors [2761]. The farfield is directly source oriented but particle motion is small and contains a 180° ambiguity (toward and away from the source), which could confound orientation. Farfield sound detection – but not

direction – is facilitated by an air bladder transforming sound pressure into vibrational motion.

Determining sound source identity, distance, and direction are three separate and important issues. Most fish detect sound in a frequency range of 20–200 Hz, those with swim bladder connections >2 kHz [1410], while clupeids of the subfamily *Alosinae* also detect ultrasound up to 180 kHz [1575]. Fish can discriminate complex sound identity [2009]. Different reef habitats make identifiable “music”, often associated with animal sounds that change with time of day, and reef fishes and their larvae are differentially attracted to these high frequency (1–2 kHz) sounds [2057,2058]. Local habitat properties and ambient noise can limit, channel, and amplify sound and modify its spectral composition, e.g. low frequency sound attenuates rapidly in shallow water [1576,2162,2405]. In open water, detection distance is inversely proportional to sound frequency; a possibly useful distance cue. Of course, all detection distances vary with source amplitude. Determining source direction is difficult when compared to terrestrial animals. Sound in water travels ~ 1500 m/s; this makes determination of arrival time differences between two larval ears (separated by 0.25 mm, Figure 1.1) problematic: sound will reach their ears <0.4 μ s apart, which is unlikely to be resolved by the brain. Also, apart from their swim bladder and otoliths, fish are almost transparent to sound, which eliminates intensity differences between the ears: fish do not cast a “sound shadow”. Finally, larvae are $1000\times$ smaller than the wavelength of their best hearing frequency (~ 100 Hz), all but eliminating detection of bilateral phase differences. Schuijf [2289] proposed early models for acoustic localization of a sound source requiring the detection of both particle motion and sound pressure, which could only be achieved by a combination of sensory organs (see below). Field experiments are still needed to test these models.

Anatomy Fish hearing is based on hair cells: extremely sensitive directional motion detectors that record three-dimensional rotational acceleration in the semi-circular canals, linear acceleration in otolithic organs (utricle, saccule, lagena), and fluid flow in and across the lateral line [2008]. The otolithic organs and lateral line canals respond to sound particle motion, while the compressible swim bladder not only regulates buoyancy but also responds to sound pressure, which it transmits as particle motion to the nearby otolithic organs. In some reef fishes, accessory structures improve hearing (increased sensitivity and extended upper frequency range) by specifically coupling the swim bladder to the ear (“otophysic” connection) via bony connections or swim bladder extensions. The lateral line assumes two forms that monitor flow and pressure variance along the head and body: superficial neuromasts are drag receptors that respond directly to flow and canal organs measure ambient pressure patterns converted to flow in the canals. Butterflyfish of the genus *Chaetodon* have a “laterophysic” connection between swim bladder and lateral line

canal [2628], which then acts as an additional sound pressure detection organ. Detailed knowledge of ear anatomy and its accessory connections can suggest hearing capabilities including the detection spectrum of sound frequencies. It follows that larvae should detect hydrodynamic sound when they have otoliths, and sound pressure when a swim bladder develops.

Anatomical–histological descriptions of haircell organs and their accessory structures are still rare for reef fish larvae. Exceptional is the recent work on larval and juvenile butterflyfish [2628]. Early larval stage (7 mm standard length (SL)) *Chaetodon ocellatus* have the full complement of semi-circular canals and otolithic organs; around the time of settlement (~15 mm SL), they also have an inflated swim bladder in close proximity to the ear and to a lateral line canal. This specialization improves sound detection threshold and higher frequency detection (from ~0.1 to >2 kHz), thus facilitating detection of animal-generated reef sound. Post-settlement, anterior swim bladder extensions (“horns”) develop which maintain the association between swim bladder, lateral line, and otolithic organs. Overall, reef fish larvae appear to hatch with near-complete otolithic organs (and semi-circular canals) and many species, including gobies (Figure 1.1) and chaetodontids, hatch with an inflated swim bladder. However, the mere presence of otoliths in hatchlings does not imply hearing, which depends on brain processing of information.

Neurophysiology Audiograms showing threshold detection across a frequency range have been measured electrophysiologically from the brain stem (known variously as ABR “acoustic brainstem recording” or AEP “acoustic evoked potentials”) of well over 100 fish species (reviewed by Ladich and Fay [1410]) including a few larval reef fishes. Pre- and post-settlement *P. nagasakiensis* larvae heard nearly equally well across the 0.1–2 kHz range and responded to locally recorded reef sounds [2739]. In the 100–500 Hz range *Abudefduf saxatilis* became less sensitive with age (>50 mm) but gained detection of higher (1–1.6 kHz) frequencies [743]. Audiograms of larvae of six species (four reef-settling and two remaining pelagic as adults) had similar shapes in the 0.1–2 kHz range with best hearing 0.1–0.3 kHz, but the pelagic species were significantly less sensitive [2742]. The authors suggest that settlement-stage larval reef fishes may be able to detect reef sounds at distances of a few 100 m, or more if AEP underestimates behavioral detection. At their best frequencies (0.1–0.2 kHz), *Chaetodon ocellatus* had detection thresholds 30–40 dB lower than in the comparably sized damselfish *A. saxatilis*; the presence of swim bladder horns in chaetodontids but not pomacentrids suggests that the threshold results could apply generally to all members of these two genera [2628].

In general, it is likely that all fish can detect the particle motion component of the sound nearfield and that the pressure component of the farfield becomes accessible to fish that have a swim

bladder, particularly if they develop direct connections between the bladder and the inner ear [2060]; lateral line canals can play an additional role [1099]. The compressible swim bladder vibrates in sync with ambient sound pressure patterns and becomes an internal sound source: hearing thresholds improve and the upper frequency range increases dramatically thereby improving detection of source distance and identity. However, the bladder’s location inside the body obscures the original source direction or, according to Schuijff [2289], could help resolve ambiguity. While physiological measurements can generate audiograms, only behavioral experiments can show orientation.

Behavior Initial experiments on sound detection were done by adding sound to light traps. Just as with light trap experiments, which have been compared to attracting moths to a candle, so are sound trap experiments subject to similar criticism: what do the larvae do under natural conditions? However, in subsequent years it has become clear that reef fish larvae can discriminate between sounds and that different marine habitats produce different sounds. As discussed above, it remains unclear how these larvae derive directional sound information. It is also not clear whether larvae are attracted to sound traps without light.

Simpson *et al.* [2363] reported greater attraction to frequencies above than below 570 Hz; the higher frequencies are associated with invertebrate sounds (e.g. snapping shrimp, grazing sea urchins). Settling larvae could also differentiate between sounds from different habitats [2058]. It is not known if this preference is innate or learned, nor how specific the “music” needs to be. Directional responses to sound were observed in captured larvae of marine invertebrates and fishes, including reef fishes, which were released and observed in the field. Depending on location and time of day some showed attraction, others avoidance of the sound source some meter(s) away [1456,2361,2507]. A clear example of the curved orientation path in the nearfield was shown in adult *Porichthys notatus* females locating a dipole point source over short distances [2761]. This behavior appears guided by the oscillating hydrodynamic flow detected by the inertial otolith system as the sound waves move the entire animal. It may apply in principle to fish larvae, although reef sound dispersal fields are not comparable in either shape or distance to a nearby dipole point source in speaker tests [2059,2405]. This can confound interpretation regarding orientation and needs to be taken into account in reef sound studies.

In sum, reef fish larvae hatch with clearly differentiated semi-circular canals and otolithic organs and some have inflated swim bladders (Figure 1.1). Physiological audiograms show best responses around 100 Hz with sensitivities varying as much as 30 dB among damselfish species. Sound recordings have shown that reef habitats have different “music” and larvae are attracted to and can differentiate between recorded reef sounds played back from nearby speakers, particularly sound of biological

origin. The distance over which pelagic larvae can acoustically orient to reefs has been estimated at ~1 km, but this remains to be tested, as are the detection mechanisms on which this behavior is based.

Vision

Vision requires eyes, image-forming photoreceptor organs that analyse spatial and temporal light patterns. Eyes are typically composed of rhodopsin-based photoreceptors organized in a neural retina with accessory structures, prominently a focusing lens. Vertebrate retinas also contain cryptochromes, polarized molecules affected by the Earth's magnetic field (see further below). We ignore here a "dermal light sense" and a pineal organ, which could play a role in circadian and endocrine responses indirectly affecting behavior, including navigation. Eyes can be involved not only in object detection and tracking a visual flow field, but also in tracking celestial cues (sun, stars, sky polarization, etc.) and surface wave patterns.

Physical constraints Light visible to humans is electromagnetic radiation with wavelengths ~400–700 nm. The visual spectrum of fishes is not too different although several species can detect UV light [2346]. Photoreceptor neurons with different wavelength absorption spectra, including UV, form the basis of color vision. The electric wave (e-vector) oscillates perpendicular to the light beam causing light refracting into the water and reflecting off the water (and other surfaces) to become polarized. Polarized light detection requires a well-organized retina with photoreceptors aligned with different e-vectors, typically two receptor populations with perpendicular alignment of optimal photon absorption. Image formation requires photoreceptive neurons to be organized as a map that remains preserved in the brain (optic tecta of fish, e.g. Figure 1.1). Both resolution and sensitivity increase with lens size and the number, density, and organization of receptors: i.e. large eyes. Motion detection depends on neuronal "refresh" rate (flicker-fusion) and thus light intensity. Vision (color, polarization, image, and motion detection) suffers under low-light conditions and with small eyes. Water absorbs and reflects light, leading – respectively – to decreasing intensity and increasing scatter with depth. Water and its many dissolved chemical substances and suspended particles absorb different wavelengths leading to ambient "color" changes and image "fogging", greatly reducing image contrast. All these factors limit visual detection distance under water.

Anatomy Given the importance of large eyes for visual performance it is not surprising that larvae hatch with proportionally (very) large eyes and visual brain areas (Figure 1.1). It suggests that vision is of immediate behavioral importance to the hatching. However, in absolute terms their eyes are small, restricting visual performance. They aid in feeding [e.g. 1254] and perhaps

predator avoidance, but small eyes and poorly organized retinas of early pelagic larvae may also help to establish a sun compass and recognize other light patterns such as passing surface waves that do not require high-resolution vision. As the larvae grow, their eyes (lens, retina) and brain become larger and more organized.

Lara [1419] provides a detailed histological account of larval and post-larval eye morphology and visual acuity of 12 species of Caribbean labrids and scarids. Initially, larvae have a pure cone retina in an unorganized pattern. During early post-settlement, rods (associated with low-light vision) appear rapidly and cones become organized in a regular mosaic, including features associated with detection of polarized and UV light which may be used in navigation [1067] and planktonic prey detection. The spectral transmission properties of ocular media support UV detection in both pre-settlement larvae and adult reef fishes [2347]. Double cones in all recently settled juvenile labrids were arranged at 90° suggesting polarized light detection [405], which has now been shown behaviorally for post-larval anemone fish [225].

Visual sensitivity and resolution are based on lens size and number/size/density of photoreceptors. Human 20/20 vision resolves just under 1 minute of arc (arcmin) based on a smallest cone diameter of ~1 μm. In contrast, Lara [1419] found that larval scarids had rather poor visual acuities (35–87 arcmin), improving to 30–63 arcmin in juveniles and 12–21 arcmin in adults. She calculated that in daylight a settling larva could recognize a 30 cm coral head from a 12–30 m distance and that fish larvae may be able to see the edge of the reef from 100 m away in daylight, but not during the nighttime, new-moon conditions under which they settle most frequently. Perhaps settlers use vision to locate the reef during the day and after dark switch to other sensory modalities, such as sound.

Many other studies support the general developmental process of larval vision. For example, 3 dph, at the start of feeding, cones appear in the undifferentiated retina of *Glaucosoma hebraicum*; at 3–20 dph single and multiple cones develop in rows; and, at 20–90 dph, a square cone mosaic develops while rods are also added [2312]. Interestingly, eye development in *Acanthochromis polyacanthus* larvae, which do not disperse in the pelagic, is similar to that of dispersing larvae, suggesting developmental constraints on eye development with rods, cones and square cone mosaics as juveniles and adults [1914]. A contrasting example of the pelagic to benthic lifestyle change is seen in the goatfish *Upeneus tragula*, where cone density and visual acuity decreased rapidly after settlement [2310]. Larval retinas of species that are nocturnal as adults had already more rods while diurnal species have more cones [2311].

Tested in the range of 355–650 nm in a plankton-feeding assay, *Apogon compressus* and two pomacentrids showed greatest spectral sensitivity in the far blue (λ_{\max} 500 nm); this may match the