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SENSORY ENVIRONMENTS, LARVAL ABILITIES AND LOCAL SELF-RECRUITMENT

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ABSTRACT

Models of larval dispersal rarely incorporate the behavior of larvae, yet many potential settlers of marine invertebrates and fishes may navigate toward suitable settlement sites by responding to gradients of environmental stimuli. Accordingly, a variety of stimuli may be used for navigation (directed movements to the source of stimuli) and partial navigation (e.g., migration to a current that may favor transport to a settlement site) in the pelagic environment. A broad diversity of taxa have senses that allow them to detect variation in: water chemistry (biotic sources, e.g., amino acids and abiotic sources, e.g., salinity), sound and vibration (biotic sources, e.g., grunting fishes, abiotic sources, e.g., waves breaking), white light gradients and images, polarized light, current direction, magnetism and water pressure. Some organisms can detect multiple stimuli (e.g., decapods and fishes) and integrated sensory responses are likely to be common; many potential settlers of these taxa are good swimmers. Demonstrations of strong orientation to stimuli and navigation over short (centimeters to meters) and broad spatial scales (tens of meters to tens of kilometers) are most common for these groups. Partial navigation, involving vertical migration, is common for invertebrate larvae. A consequence of vertical migration can be transportation that favors movement to suitable settlement habitat. Navigation over a range of spatial scales may use stimuli that are very predictable regardless of location (e.g., water pressure, gravity). The gradients of other stimuli may be more useful for environment-specific signals and even the location of natal habitats, locations and conspecifics (e.g., using sound or smell of specific taxa). We argue that some larvae may use a hierarchy of sensory cues to find suitable settlement sites and that some of the same types of stimuli may be used at more than one spatial scale (as demonstrated for adult salmonid fishes). There are good demonstrations of the use of cues for orientation and navigation at small spatial scales (less than a few meters). More information, however, is required at spatial scales that are relevant to navigation over kilometers before behavior can be incorporated more accurately into models of larval dispersal.

The bipartite life history of most marine invertebrates and fishes generally results in a decoupling of presettlement forms from spawning adults and the environment occupied by adults. Invertebrate larvae may spend minutes to months in the pelagic environment (Davis, 1987; Scheltema, 1986), while reef fishes may have a presettlement phase of 10 to 120 d (Brothers et al., 1983; Leis and McCormick, in press). Larvae must locate, or be transported, to a suitable environment before they settle.

Knowledge of the sources and sinks (i.e., settlement sites) of presettlement invertebrates and fishes is fundamental to understanding units of management of marine resources. Settlement into coastal or isolated reef environments may depend on the presence and strength of cues to which the larvae may respond. If larvae have presettlement phases of days to months then the probability of returning to a natal area (= area from which spawned/born) is likely to be low if information cannot be gained on the direction of suitable habitat and, possibly, the distance from it. We know that larvae sometimes return to natal reefs (Jones et al., 1999; Swearer et al., 1999), but we do not know how this is accomplished. Although oceanography can favor recruitment to natal environments at scales encompassing tens of meters (eddies, McShane, 1996), kilometers to tens of kilometers (linear oceanographic features, Kingsford, 1990; Grimes and Kingsford, 1996; stratified flows, Cowen et al., 2000) and tens of kilometers to hundreds of kilometers (Lee and Williams, 1999) this is unlikely to be the full story (Kingsford and Finn, 1997; Wolanski et al., 1997). Armsworth (2000) concluded that hydrodynamically based considerations of incidental recruitment, or passive entrainment, appear less important than consideration of larval swimming. Although many presettlement forms of invertebrates are weak swimmers (Chia et al., 1984; Young, 1995) some invertebrates (Zeldis, 1985; Lukenbach and Orth, 1992) and fishes (Leis and Carson-Ewart, 1997) should really be considered as micronekton rather than plankton because they have a high level of mobility, particularly near the end of the presettlement phase. In addition, many of these organisms have sensory systems that are capable of using a variety of physical and biological cues (Hara, 1994) that would provide information on the location and sometimes distance of natal habitat, or more generic suitable settlement sites (e.g., any reef, not necessarily the natal reef).

There are multiple physical and biological cues that could be used by organisms (including larval forms) in the marine environment and their concentrations, gradients, frequencies or intensities can vary in a way that is useful for orientation. Chemical stimuli, with directional information, may be found in environments from estuaries to hydrothermal vents (Mullineaux and France, 1995). Variation in ambient noise and vibration is considerable and biological (e.g., snapping shrimps, fishes) and physical sources (waves) may be relatively predictable in space and time (Rogers and Cox, 1988; Janssen et al., 1990; Cato, 1992). Visual cues including celestial bodies and related polarized light and directional light may also provide cues (McFarland, 1986; Thorson, 1964). Local variation in magnetic fields due to magnetic anomalies preserved in volcanic rocks is considerable and is potentially useful for navigation (e.g., salmonids, Quinn and Dittman, 1990), as is, of course, the earth’s magnetic field.

Our knowledge of how these senses are used by larval forms for orientation and choice in the pelagic environment, however, is largely speculative. Navigation or orientation to cues has rarely been incorporated into models of larval dispersal (but see Wolanski et al., 1997). Although cues are often discussed in isolation, we argue that it is likely that multiple cues are used and the relative importance of them may change with distance from the source. Adult salmonids, for example, use magnetic cues at scales of hundreds to thousands of kilometers, positive chemotaxis to natal rivers at hundreds of meters to kilometers, positive rheotaxis during migration upriver, combined with chemotaxis for conspecifics at scales of meters to tens of meters (Quinn and Dittman, 1990). Larval fishes and invertebrates are clearly influenced by cues close to settlement (Sweatman, 1983; Svane and Young, 1989; Hadfield and Strathmann, 1996) and have the necessary sensory morphology for broader scale detection of suitable settlement sites. It is likely, therefore, that an understanding of both swimming and sensory abilities is crucial in estimating the probability of specific taxa being able to settle in a natal environment.

Our objectives are to: (1) describe variation in the sensory environment that could be used by presettlement forms for orientation and navigation); (2) describe the sensory abilities and behavioral responses of organisms to variation in the sensory environment including the integration of multiple sensory sources; and (3) comment on the spatial and temporal scales at which sensory information may be used based on the sensory abilities of the early life history forms.

Early Life History and Orientation.—We use the term presettlement phase (sensu Kingsford and Milicich, 1987) to refer to all of the developmental stages from hatching to settlement. The presettlement phase may include larvae, post larvae and pelagic juveniles (as for fishes, Leis and Rennis, 1983). In some cases we have referred to 'potential settlers', these are late-stage presettlement forms. We have avoided the term 'competent' (cf 'potential settler') because it is functionally difficult to categorize wild presettlement forms in this way, although we recognize that in some cases it is possible to do so.

We describe the orientation of taxa to different cues, but orientation takes a number of forms. We consider it highly unlikely that presettlement forms can 'home' (sensu Papi, 1992) to the exact location from which they were spawned. Given that presettlement reef fish can settle on reefs that range in size from hectares to square kilometers (Jones et al., 1999) it is likely that orientation and movement constitutes navigation (i.e., control their position and course to a suitable environment) to a natal reef. It is also likely that they can navigate to environments that are suitable for settlement that are not natal (i.e., other reefs). The larvae of some organisms may not navigate, but orient themselves in such a way that there is a higher probability of survival through physical transport to a suitable environment and, in some cases (perhaps by accident), their natal habitat. This may be the case in partially enclosed water masses (e.g., estuaries and embayments; Rothlisberg et al., 1996) or shelf waters. For example, by orienting in a stratified flow, through vertical migration, larvae may move away from the shore and later position themselves in a water mass that facilitates onshore transport. This approach has a high probability of success on extended coastlines of similar oceanography and orientation (e.g., lobster phyllosoma, Phillips, 1981; barnacle larvae, Pineda; 1999; fish larvae, Cowen et al., 2000). It is also possible that some larvae use the latter approach (partial navigation) and then navigate over short spatial scales (meters or less) to suitable habitat in which to settle. Some taxes are discussed with respect to the broader implications of transport through partial navigation. Our emphasis is on navigation.

Organisms sense their environment and alter their behavior accordingly. We have attempted to depict the ontogeny of sensory ability by indicating what is known about early, mid and late in the presettlement phase (Table 1). Sensory information may allow organisms to respond to near (within a few body lengths) or distant cues. Evidence for sensory abilities may be in the form of morphological descriptions of the relevant organs, or, more convincing, physiological or behavioral demonstrations of sensory organ operation. The most compelling evidence is that an animal actually uses sensory cues to orient in a way that could potentially aid in attraction or navigation. We focus on the abilities of presettlement forms of benthic marine species, but if information is lacking on these, we include information on other stages (including adults) or species in the same broad taxonomic group. Special emphasis is given to some groups, such as decapods, where there are good data and the presettlement phases are diverse in morphology (e.g., lobster phyllosoma versus crab megalopa). During the pelagic larval stage of many marine animals, both growth and development take place. Thus both sensory and swimming abilities are constantly changing, and can be expected to increase between hatching and settlement. The degree of change and its trajectory are taxon-specific and little understood. Obvious exceptions to this statement include presettlement invertebrates such as solitary ascidians (Svane and Young, 1989).

Table 1. Sensory abilities and responses of marine fishes and invertebrates. An entry indicates presence in at least one species. Nearfield means an object within less than 5–10 body lengths, and farfield is beyond that. M, morphological evidence of sensory organ function; A, sensory ability demonstrated behaviorally or physiologically; ON, sense used in orientation in nearfield only; OF, sense used in orientation in farfield.* only in a species lacking a pelagic, dispersive larval stage (e.g., shark), or in a freshwater species (e.g., trout). Vision, a photoresponse or image-forming eyes (respond to 'environmental' or 'celestial' cue).

Organism	Sense	At hatch	Mid-pelagic	Potential settlers	Juvenile	Adult	Examples
Sponges							
	Olfactory						Leys, pers. comm.
	Vision – Environmental		A, ON	ON			Maldonado and Young, 1996; Maldonado et al., 1997
	Water movement						
	Gravity						Svane and Dolmer, 1995
Cnidarians							
	Olfactory						
	Vision – Environmental	A, ON					Siebert, 1974; Svane and Dolmer, 1995
	Water movement						
	Gravity						Svane and Dolmer,1995
Bryozoans							
	Olfactory		M, ON	A, ON			Maki et al., 1989
	Vision – Environmental	A, ON	M, A, ON	A, ON			Hughes and Woollacott, 1978
	Temperature			ON			Yoshioka, 1973
	Gravity		A, ON				Pires and Woollacott, 1983
Polychaetes							
	Olfactory			ON			Pawlik, 1986; Gee 1965; Scheltema et al., 1981
	Vision – Environmental	A, ON	A, ON	A, ON			Marsden, 1986; Young and Chia, 1982
	Water movement			A, ON			Pawlik and Butman, 1993
	Salinity			A, ON			Lyster, 1965
	Pressure		A, ON				Knight-Jones and Morgan, 1966
	Thigmokenisis			A, ON			Marsden, 1988
	Gravity		A, ON				Wilson, 1982

Table 1. Continued.

Organism	Sense	At hatch	Mid-pelagic	Potential settlers	Juvenile	Adult	Examples
Bivalves							
	Olfactory			A, ON			Tamburri et al., 1992, 1996; Hidu, 1969
	Vision – Environmental	A, ON	A, ON	A, ON			Xu and Wang, 1990; Leslie and Wilson, 1983
	Water movement						Carriker, 1951, 1961; Jonsson et al., 1991
	Temperature		A, ON				Mann and Wolf, 1983
	Salinity	A, ON	A, ON	A, ON			Mann et al., 1991
	Pressure		A, ON	A, ON			Bayne, 1963; Mann and Wolf, 1983
	Gravity	A, ON	A, ON				Bayne, 1964; Xu and Wang, 1990,
Gastropods (non-opistobranch)							
	Olfactory			A, ON	ON		Morse et al., 1979; Davis and Stoner, 1994
	Vision – Environmental	A, ON	A, ON				Barile et al.,1994; Yano and Ogawa, 1977; Yano, 1981
	Water movement						
	Temperature	A, ON	A, ON				Yano and Ogawa, 1977
	Salinity	A, ON	A, ON				Yano, 1981
	Pressure	A, ON	A, ON				Digby, 1967; Yano and Ogawa, 1977
	Gravity	A, ON	A, ON				Barile et al., 1994
Gastropods (opistobranch)							
	Olfactory						Thompson, 1958; Gibson, 1995; Murphy and Hadfield, 1997
	Vision – Celestial					A,ON	Hamilton and Russell, 1982 Adult *Aplysia* and *Tritonia*
	Magnetic					A,ON	Lohmann and Willows, 1987 Adult *Aplysia* and *Tritonia*
	Water movement					A,ON	Hamilton, 1986 Adult *Aplysia* and *Tritonia*
Cephalopods	Olfactory					M, A, OF	Williamson, 1995
	Auditory						Pakard et al., 1990; Williamson, 1995
	Vibration					M, A, OF	Williamson, 1995
	Vision – Environmental					M, A, OF	Williamson, 1995
	Pressure		A, ON				Rice, 1964
	Thigmokinesis					A, ON	Williamson, 1995
	Salinity	A, ON	A, ON	A, ON			Forward, 1989; Tankersley et al., 1995
	Pressure	A, ON	A, ON	A, ON			Sulkin, 1990, 1984; Tankersley et al., 1995
	Thigmokinesis			A, ON			Kingsford and Choat, 1985; Shanks, 1985

Table 1. Continued.

Organism	Sense	At hatch	Mid-pelagic	Potential settlers	Juvenile	Adult	Examples
Crustacea Barnacles							
	Olfactory			A, ON			Crisp and Meadows, 1962; Yule, 1986
	Vision – Environmental	A, ON	A, ON	A, ON			Lang et al., 1979
	Water movement			A, ON			Pineda, 1994; Mullineaux and Butman, 1991
	Pressure	A, ON	A, ON	A, ON			Rice, 1964
	Gravity		A, ON				Wilson, 1982
Crustacea Crabs							
	Olfactory			A, ON			Diaz et al., 1999; Christy, 1989
	Vision – Environmental	A, ON	A, ON	A, ON	A, ON	A, ON	Forward and Cronin, 1979; Shanks, 1985
	Vision – Celestial			A, ON	A, ON	A, ON	Altizer and Forward, 1993; Shanks, 1995
	Water movement		A, ON	A, ON			Shirley and Shirley, 1988; Shanks, 1995
	Temperature	A, ON	A, ON	A, ON			Ott and Forward, 1976; Forward, 1990
	Salinity	A, ON	A, ON	A, ON			Forward, 1989; Tankersley et al., 1995
	Pressure	A, ON	A, ON	A, ON			Sulkin, 1990, 1984; Tankersley et al., 1995
	Thigmokinesis			A, ON			Kingsford and Choat, 1985; Shanks, 1985
	Gravity	A, ON	A, ON	A, ON			Sulkin, 1990, 1984; Shanks, 1985
	Polarized light	A, ON	A, ON	A, ON	A, ON	M, ON	Via and Forward, 1975; Shaw, 1966
Crustacea Shrimp							
	Olfactory			A, ON	A, ON		Benfield and Aldrich, 1992
	Vision – Environmental	A, ON	A, ON	A, ON	A, ON		Wilson et al., 1999; Hughes, 1972
	Vision – Celestial			A, ON	A, ON		Ugolini et al., 1989; Goddard and Forward, 1989
	Temperature						Rogers et al., 1993
	Salinity			A, ON			Hughes, 1969
	Pressure			A, ON	A, ON		Baylor and Smith, 1975; Forbes and Benfield, 1986

Table 1. Continued.

Organism	Sense	At hatch	Mid-pelagic	Potential settlers	Juvenile	Adult	Examples
Crustacea							
Lobsters							
	Olfactory					M, A, ON	Weaver and Atema, 1998; Boudreau et al., 1993
	Auditory			M, ON			Phillips and MacMillan, 1987; MacMillan et al., 1992
	Vibration			M, ON	M, ON	M, ON	Jeffs et al., 1997; Phillips and Macmillan, 1987
	Vision – Environmental	A, ON	A, ON	A, ON	M, ON	M, ON	Ennis, 1973; Ritz, 1972
	Magnetic					A, ON	Lohmann et al., 1995
	Water movement			A, ON		A, ON	Cobb et al., 1989; Nevitt et al., 1995
	Temperature	A, ON	A, ON				Boudreau et al., 1991
	Salinity						Scarrat and Raine, 1967
	Pressure	A, ON	A, ON				Ennis, 1973
	Thigmokinesis			A, ON	A, ON		Shojima, 1963; Herrnkind et al., 1976
	Gravity			A, ON			Sekiguchi and Terazawa,1997
	Polarized light				M, ON	M, ON	Meyer-Rochow, 1975
Echinoderms (where larval stage not clear, used mid-pelagic)							
	Olfactory			ON		M, A, ON	Burke, 1984; Kitamura et al., 1993
	Vision – Environmental		A, ON				Pennington and Emlet, 1986
	Water movement						
	Salinity			ON			Metaxas and Young, 1998
	Gravity		A, ON				Yamaguchi, 1977

Table 1. Continued.

Organism	Sense	At hatch	Mid-pelagic	Potential settlers	Juvenile	Adult	Examples
Ascidians (note all stages are potential settlers)							
	Olfactory			M, ON			Svane and Young, 1989; Grosberg, 1981
	Vision – Environmental			M, A, ON			Svane and Young, 1989; Duyl et al., 1981
	Water movement			A, ON			Davis and Butler, 1989; Stoner, 1990
	Temperature						
	Salinity						Vasquez and Young, 1996
	Gravity			M, A, ON			Svane and Young, 1989; Pires and Wollacott, 1983
Fishes	Olfactory		M, A	M, A, OF	M, A, OF	M, A, OF	see text
	Auditory	M	M, A	M, A, OF	M, A, OF	M, A, OF	"
	Near-Field Vibration	M, A, ON	M, A, ON	M, A, ON	M, A, ON	M, A, ON	"
	Vision – Environmental	M, A, ON	M, A, OF?	M, A, OF	M, A, OF	M, A, OF	"
	Vision – Celestial	M	M	M, A, OF	M	M, A	"
	Magnetic				A, OF	M, A, OF	"
	Water movement	M,A,	M, A, ON	M, A, OF	M, A, OF	M, A, OF	"
	Electrical				M*, A*, OF*	M*, A*, OF*	"
	Temperature	A,ON	A,ON	A, ON	A, ON	A, OF	"
	Pressure	A,OF	A,OF	A, OF	A, OF	A, OF	"

SENSORY AND LOCOMOTORY ABILITIES

The ability of organisms to use sensory cues, at different spatial scales, depends on the presence of relevant sense organs, the sensitivity of organs, the ability to determine direction, the behavioral responses to cues and their mobility (Atema, 1988; Blaxter, 1988). It may be possible for organisms to detect cues at great distances from a source, but unless they can move toward the source, the cue cannot be considered to have a major role in navigation. If such cues are used by organisms at multiple spatial scales then low threshold sense organs and good locomotory abilities are prerequisites for successful navigation to the source. The pelagic juveniles of reef fish or lobster pueruli, for example, will have greater sensory and locomotory abilities than sponge larvae (Phillips and Sastry, 1980; MacMillan et al., 1992; Maldonado and Young, 1996; Stobutzki and Bellwood, 1997; Leis and Carson-Ewart, 1997). A simple comparison among taxa is provided in Figure 1.

The relationship between mobility and number of senses largely focuses on potential settlers (Fig. 1). Most larvae hatch from eggs at very small sizes (e.g., fishes ~1.5 to 5 mm, crustaceans 0.05 to 1 mm), have weak powers of locomotion and more limited sensory abilities early in life (Table 1). Even at these small sizes, organisms such as fishes have functional senses including olfaction and vision. We would argue, however, that their powers of detection and ability to respond to distant cues must be more restricted than for larger fishes.

ENVIRONMENTAL STIMULI AND SENSORY RESPONSES

CHEMISTRY AND PHYSICAL OCEANOGRAPHY.—Many developmental phases of invertebrates and fishes have sensory abilities that would allow them to gain information on the direction and potentially the distance of targets based on chemotaxis (Table 1). Marine vertebrates (turtles, Grassman et al., 1984; salmonid fishes, Quinn and Tolson, 1986) and invertebrates (Atema and Cowan, 1986) are known to respond to small variations in water chemistry. It is also known that many larvae are chemotactic, especially close to settlement where decisions are made on scales of less than a few meters (barnacles, Crisp and Meadows, 1962; polychaete worms, Pawlik, 1986; reef fish, Elliott et al., 1995). How senses are used by larval forms for orientation and choice at larger spatial scales (hundreds of meters to tens of kilometers) in the pelagic environment is largely speculative.

There is great variation in the chemical composition of marine waters at small (millimeters to meters) and large (hundreds of meters to kilometers) scales and multiple sources provide potential cues for larval navigation and the choice of settlement sites. Fish and some invertebrates respond to differences in concentrations of amino acids, fatty acids (molecular components of lipids, including steroids), alcohols, salinity and temperature (Kobayashi and Fujiwara, 1987; Mann et al., 1991). We include temperature here, because salinity and temperature combine to influence water density and temperature can affect the dispersal and activity of chemical stimuli.

Billen et al. (1980) concluded that dissolved organic carbon (DOC) compounds, to which organisms may respond, mostly weigh 3000–5000 Daltons and fewer than 10% weigh less than 500 Daltons (e.g., amino acids and monosaccharides). The proteins, polysaccharides and lipids that make up the bulk of the DOC diffuse more slowly than lighter molecules and, therefore, generate longer-lasting chemical gradients (Atema, 1988).

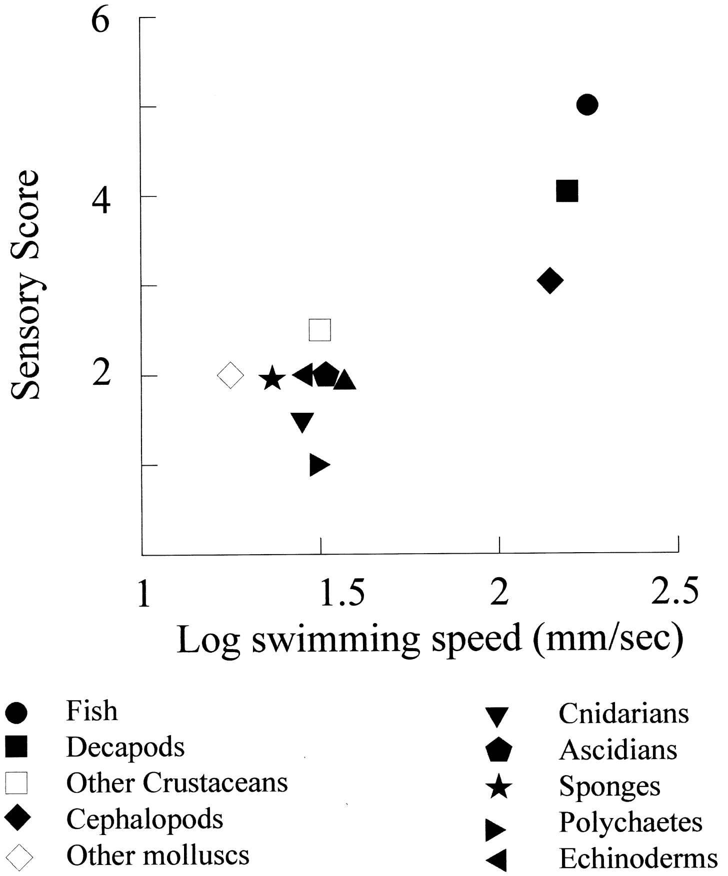

Figure 1. The relationship between vagility (represented as swimming speed) and sensory abilities for potential settlers of 11 marine taxa. The senses that contributed to the scores were: hearing, vision (non-image forming), vision (image forming), olfaction, magnetic and electrical senses. Swimming speeds are from papers cited in Sponaugle et al., (this issue). The sensory score is based on information in Table 1 for six types of sensory information thought to be important to orientation: hearing, image-forming vision, non-image forming vision, olfaction (including any dissolved substance, e.g., salinity), magnetic sense, electrical sense. For each taxon, a score of 1 was given for each sense present in larvae, 0.5 for each sense not known in larvae, but known in adults, and 0 for each sense not known in either adults or larvae. It is important to note that, especially in invertebrates, some senses may not have been examined.

Amino acids and free fatty acids may be consumed quickly by bacteria. Chemical gradients of large molecules (i.e., over 3000 Daltons) may have a halo of breakdown products (e.g., amino acids) that may be important for chemotaxis. Although fishes respond to alcohols, and there are many sources of alcohols in marine environments (e.g., manitol in algae, Gillanders and Brown, 1994), sensitivity to alcohol is weak compared to other compounds (Hara, 1994). In contrast, fishes can orient to very low concentrations of amino acids (Kobayashi and Fujiwara, 1987). Invertebrates (e.g., lobsters) and fishes (Lara, 1999) often have bilateral sensing for chemical stimuli; this morphology is best suited for orientation to chemical gradients (Basil and Atema, 1994). Bilateral sensing can be used to detect fine scale gradients and turbulence in seemingly uniform chemical plumes (Moore and Atema, 1991).

The factors influencing the distribution of chemical stimuli vary with spatial and temporal scales (Atema, 1988). At tiny spatial scales (<mm) and over brief periods (seconds) diffusion dominates, while at larger spatio-temporal scales the dispersal of stimuli is dominated by fluid motion. Chemotaxis may be relevant to settling organisms at small spatial scales (e.g., some invertebrate larvae), but the larger spatial scales are of more relevance to navigation. Diffusion gradients are predictable, but the behavior of chemical stimuli in currents is less predictable and prediction is dependent on 'averaging' of signals (Atema, 1988). It is likely that temporal variation in concentrations of chemical stimuli will be great and this has the potential to influence the numbers of larvae that successfully settle. This variation may range from years to seasons and through stochastic events (e.g., rainfall) and the biology of organisms releasing exudates.

The influence of oceanographic features on the larval stages of invertebrates and fishes has received great attention (e.g., Denman and Powell, 1984; Kingsford, 1990; Mann and Lazier, 1991; Shanks, 1995; Cowen et al., 2000). This literature has emphasized onshore and offshore transport, retention, and interactions with predators and prey. Oceanographic features may also influence concentrations of biotic and abiotic chemical stimuli and the directional information that chemicals provide. Oceanographic features are likely to have unique chemical signatures that include metabolites of organisms (nutrients, amino acids and monosaccharides), lipids and proteins that are the breakdown products of decomposition. Other compounds that characterize water masses may include manitol from algae, tannins from terrestrial plants and even pollutants (Kingsford and Gray, 1996). The lagoons of coral reefs, for example, are rich in the mucous and DOC of corals and other organics (Davies and Hughes, 1983) and this material is advected out of the lagoon in turbidity plumes that are tens of meters to kilometers in length (Booth et al., 2000; Kingsford, unpubl. data). Ebb-tide waters from the continental shelf of the Great Barrier Reef and lagoons in other coral reef systems (Wolanski, 1994) may generate chemical gradients to which larvae in the Coral Sea could respond. Plumes are generated by rivers and estuaries that may produce clear chemical stimuli. These features may disperse kilometers and even tens of kilometers into mainstream currents (review Grimes and Kingsford, 1996). Convergences could, in some cases, guide larvae along concentration gradients back to a point source of accumulates (e.g., topographic fronts, Kingsford et al., 1991; riverine plumes, Kingsford and Suthers, 1996).

In addition to chemical stimuli of biotic origin, there are also abiotic stimuli such as changes in salinity, temperature and even concentrations of calcium carbonate from reefs (Davies and Hughes, 1983). Unique combinations of salinity and temperature often define water masses (Mann and Lazier, 1991) and can provide excellent cues. Differences in salinity and temperature are found on both vertical and horizontal planes. Estuarine plumes, for example, are characterized by conspicuous vertical and horizontal gradients in salinity and/or temperature that could be utilized by larvae to find suitable habitats (Forward, 1989; 1990; Morgan et al., 1996; Lindeman et al., 2000). Lower salinity may provide a continental signal, due to drift from rivers and local runoff (e.g., Sabates, 1990). Within shelf waters there are commonly gradients of turbidity, salinity, temperature, plankton abundance and diversity (Barnett and Jahn, 1987) and odor that may serve as orientation cues (fishes, Miller, 1988; Boehlert and Mundy, 1988). At smaller spatial scales (kilometers) the thermal signals from the lagoons of coral reefs may provide directional cues (Boden, 1952; Doherty et al., 1996). Variation in salinity and temperature with depth may also provide crucial information on the current direction and water source that may be used by larvae (Hughes, 1969). For example, the presence of low-density water and its flow would indicate an estuarine/riverine source.

Many invertebrates and fishes have the necessary morphology for chemotaxis and behave in ways that indicate that it is used for orientation (Table 1). At small spatial scales early larval forms may use chemotaxis to detect food (herring larvae, Dempsey, 1978; larval cod, Døving et al., 1994) and suitable settlement sites (crabs, Welch et al., 1997; fishes, Sweatman, 1983). The potential settlers of invertebrate larvae are attracted to particular substrata based on chemical cues (e.g., algal exudates, abalone, adults of barnacles, sand dwelling polychaetes, oysters and echinoderms, Table 1) and avoid settling on particular organisms such as sponges (Davis, 1987). The active compounds of attraction include peptides, phenols, polyssaccarides and free fatty acids (Burke, 1986; Pawlik, 1986). Chemical cues may or may not induce metamorphosis (Burke, 1986; Jensen et al., 1990) and in some cases the inducers are absorbed to the substrate so that larvae have to contact the substrate before metamorphosis can occur.

Habitats which are generally characterized by 'habitat forming' organisms (e.g., kelp, coral) may have unique chemical signatures. Although much of the evidence for the chemotactic detection of specific taxa is at small spatial scales, this sensory ability has implications for broader scale detection of habitats. Some fish may only settle at night on preferred substrata (Munday et al., 1997). Elliott et al. (1995), for example, found that damselfish larvae were attracted to anemones when they were up to 8 m downcurrent of the anemone. This response was not found to the side of the anemone, indicating the importance of the currents for transporting the chemical stimuli. Some choices are so specific that, in one case, gobies chose among coral species that were not visually recognizable as different species (Munday et al., 2001). Choice of habitat with conspecifics has been demonstrated for humbug damselfishes that settle at night and this chemotactic response appears to be concentration dependent (i.e., number of new settlers increases with density of adults, Sweatman, 1983, 1985).

Most of the evidence that larva1 responses to chemical cues influence the chance of successful settlement at great distances is through vertical migration; we consider this to be partial navigation. Some crab larvae, for example, respond to vertical salinity gradients and move to waters that favor transport to the upper reaches of estuaries (Tankersley et al., 1995). These crab megalopae are sensitive to changes in salinity as small as 5×10^{-4} psu s^{-1}. Japanese flounder larvae behave similarly and move higher in the water column with rising salinity (Burke et al., 1995). Interactions between biotic and abiotic chemical constituents have also been found to influence orientation. For example, glass eels of *Anguilla anguilla* are attracted to odorants only at low salinities (Sola and Tongiorgi, 1996).

Variation in the presence and concentration of chemical stimuli mean that natal environments may have unique chemical signatures that could attract presettlement forms. There are three criteria that generally need to be met before this is possible: (i) Eggs or larvae must be imprinted with the chemical characteristics of the waters before the presettlement phase commences. (ii) Presettlement phases must remain close (i.e., minimal dispersal) to the natal environment or, if larvae disperse from a natal environment they must be retained and/or have the mobility to interact with oceanographic features in such a way that they can return to the natal environment. (iii) Potential settlers must recognize the chemistry of the natal environment and orient towards it. Chemotaxis meets all of these criteria for some organisms. In salmonids, the juvenile stages (smolt), and even the eggs (Quinn and Dittman, 1992), may imprint to their natal rivers prior to dispersal hundreds of kilometers (Dittman and Quinn, 1996). Although the salmon appear to use magnetic senses for long distance navigation in the open ocean, chemotaxis is used on a scale of tens of kilometers as a number of rivers may be checked (Quinn et al., 1991). Imprinting is not unique to salmonid fishes. Arvedlund and Nielsen (1996) found that anemonefish larvae that had been raised in 'anemone juices' were more likely to be attracted to an anemone as potential settlers than larvae raised in the absence of juices. For some potential settlers reef specificity may not be necessary if they do not disperse more than tens of meters from adult habitat. Some invertebrates (e.g., ascidians, Davis, 1987) and even reef fish (Gobiesocidae, Kingsford and Choat, 1989) apparently disperse such short distances that the use of chemotaxis alone for the location of suitable settlement sites is possible.

SOUND.—Sound propagates well in water, but the distance it travels while still detectable depends on five main factors: frequency, intensity, water depth, background noise and receiver sensitivity. All other things being equal, lower frequencies propagate better than high frequencies. Therefore, a high-frequency sound like a snapping shrimp 'click' will not travel as far as the crash of breaking waves. Ambient noise in the ocean between 50 to 5000 Hz is predominantly biological (Cato, 1992), but also includes noise generated by wind and waves, and in some situations anthropogenic sound. Biological noise in the ocean can exceed 90 dB, and whales can emit sounds in excess of 180 dB (Cato, 1992; Pain, 2000). Sounds travel further in deep water because shallow water attenuates longer wavelengths and lower frequencies. The strength of a sound signal must exceed background noise to be detectable. In coral reef waters, background noise levels are high, and wind noise can add considerably to this. Some biological sound from reefs still exceeds background sound levels at 4–20 km from its source (McCauley, 1997). Myrberg and Fuiman (in press) suggest that the threshold of hearing is "usually 15–20 dB above the spectrum level of background noise", but Fuiman et al. (1999) found a startle response in red drum larvae at only 5 dB above background.

Fish can hear over a relatively wide range of frequencies, primarily between 50 and 5000 Hz, with best performance below 1000 Hz (Mann et al., 1997; Popper and Carlson, 1998; Fay and Popper, 1999). However, infrasounds of <20 Hz can be heard by some fishes (Myrberg and Fuiman, in press), and somewhat unexpectedly, Mann et al. (1997) recently demonstrated that a clupeid fish can hear sounds to over 180,000 Hz. This high frequency of detection opens up many previously ignored possibilities. Hearing sensitivities in marine invertebrates are virtually unknown, and there is no evidence that larvae of any invertebrate can hear. Auditory thresholds of fishes vary among species and frequencies, and differences in sensitivity among species at a given frequency as can vary by 60–80 dB. However, hearing in the most sensitive adult fishes is as good as in the most sensitive terrestrial birds and mammals (Fay and Popper, 1999).

Physical and biological sound in the sea varies temporally and spatially in both predictable and stochastic ways. Physical sources like breaking waves vary daily and seasonally. Biological sources vary on multiple temporal scales, ranging from diel differences, connected with the daily activity patterns of animals, to seasonal patterns, possibly based on reproduction (Cato, 1978, 1992; Pain, 2000). Spatial variation in sound is possibly more predictable, since physical sources like waves breaking on reefs are fixed in position, and there are normally strong correlates between habitat and the distribution of the species that are the biological sound sources. Species-specific sounds are known in some fishes

(Myrberg and Fuiman, in press), and these sounds might enable potential settlers to locate, and either approach or avoid, a given species (including conspecifics) at multiple spatial scales.

The hearing abilities of presettlement fishes or invertebrates are not well known. Most of the published works are of morphological studies that show a sensory structure is present, but without linked physiological or behavioral observations that show its functionality or detection abilities. However, the otic capsule is present and apparently functional, at least for equilibrium perception, at or very shortly after hatching in most fishes (Blaxter, 1986; Myrberg and Fuiman, in press). 'Startle responses' to sound (consisting of changes in swimming speed and direction) are known for Sparidae and Sciaenidae as small as 6–8 mm and ~20 d old (Ishioka et al., 1987; Fuiman et al., 1999). Most perciform fish larvae have gas in their swim bladders by the time the fins are formed at 3–7 mm, and an inflated swim bladder greatly increases the ability of a fish to hear underwater (Myrberg and Fuiman, in press). Tolimieri et al. (2000) showed that larvae of tripterygiids (a family of blennioid fishes common on reefs in tropical and southern hemisphere temperate waters) of 20 mm mean length can hear reef sounds and respond to them. In contrast, Myrberg and Fuiman (in press) noted that small (ca 12 mm) immediately post-settlement *Pomacentrus* of two species had poor hearing, and concluded that for these species an auditory sense is unlikely to be helpful in finding a reef.

Because of the high speed of sound in water and the small spatial separation of the ears of fishes, it is frequently assumed that fishes should be unable to localize and orient to sounds and use them for orientation (van Bergeijk, 1967). However, localization has been demonstrated in some adult fishes, and it is clear that the mechanism used by fishes to localize sound differs from that used by vertebrates in air (Popper, 1995). Suffice to say, mechanisms do exist for fishes to localize sound (reviewed in Fay and Popper, 1999), but aside from one paper, neither sound localization, nor the full morphological 'hardware' necessary for the job have been demonstrated in fish or invertebrate larvae. As noted above, Tolimeri et al. (2000) clearly demonstrated under field conditions that larvae of one species of reef fish can hear and are attracted to the sounds produced on reefs, but the distance of detection was unknown. Crustaceans can detect vibrations (copepodites, Heuch et al., 1990) and there has been long-standing speculation that lobster larvae can detect and use underwater vibrations for orientation. This has been fuelled in part by the apparent attractiveness to lobster larvae of noisy power-plant seawater intakes (summarized by Jeffs et al., 1997); definitive evidence, however, is lacking.

MAGNETIC FIELDS.—Magnetic fields pervade all environments and they range in size from those of the entire earth to small-scale variations due to local changes in the rocks of the ocean floor (Wiltschko and Wiltschko, 1995). In theory, magnetic fields could be used to distinguish east from west, to locate an oceanic island, or to navigate through local topography (Walker et al., 1992). Magnetic signals do not vary at ecological time scales, and there are certainly fixed spatial patterns of magnetism. Magnetic signatures are not usually associated with particular habitats, except that volcanic islands of different ages (i.e., paleomagnetic fields) or recent lava flows might be distinguishable from other types of islands or rocky bottoms. A number of marine organisms ranging from bacteria to large organisms, including migratory fishes like salmon and tunas as well as sharks and turtles, are able to detect magnetic fields and to use them for orientation (Wiltschko and Wiltschko, 1995; Goff et al., 1998; Table 1). The identification of the magnetic sense organ of detection has been elusive, but Walker et al. (1997) have recently identified the region of the head that contains the magnetic detection organ in salmon. Although juvenile salmon of about the same size as settlement-stage reef-fish larvae can detect and orient to magnetic fields (Wiltschko and Wiltschko, 1995), what is lacking is any indication that larval stages of marine animals can detect magnetic fields. Adult plaice in the North Sea actively orientate to external cues, most likely the electrical fields generated by flow of sea water through the earth's geomagnetic field, or the geomagnetic field itself (Metcalfe et al., 1993). Compass orientation has been observed in juvenile grunts (a reef fish, family Haemulidae), although Quinn and Ogden (1984) were unable to determine if the compass was solar or magnetic.

ELECTRICAL FIELDS.—Electrical fields exist at hugely different scales ranging from those generated at the skin/water interface of all aquatic animals (Ryan, 1980) to those generated by ocean currents (a conductor) moving through the earth's magnetic field (von Arx, 1962). The biologically-generated electrical fields vary over small spatial (millimeters to centimeters) and temporal scales and as such would be of limited use for orientation and navigation. Because electrical fields generated by ocean currents are more predictable, they have more obvious utility for orientation than do the biological sources.

Elasmobranchs and bony fishes of three primarily freshwater orders (Gymnotiformes, Osteoglossiformes, and Siluriformes, some marine catfishes; Webb, 1999) can detect electrical fields (Myrberg and Fuiman, in press), but this sense is not known in any marine vertebrate or invertebrate with pelagic larval stages. The stargazer *Astroscopus y-graecum* has an electric organ that discharges during feeding, but the function of this discharge is unknown, nor is it known if conspecifics can detect the discharge (Pickens and McFarland, 1964). The discharge is apparently not used in electrolocation (Bone et al., 1995). The electric organ is apparently present in very young, probably presettlement, stargazers (Dahlgren, 1927), but whether it is functional at this size is unknown.

Most research has focused on electrolocation of prey, conspecifics or potential predators in the vicinity (Myrberg and Fuiman, in press), and location at this scale is of limited relevance to dispersal/retention. However, larger scale orientation is at least theoretically possible in animals with the ability to sense electrical fields.

LIGHT.—Light is present in most shallow marine environments in wavelengths ranging from infrared to ultraviolet (McFarland, 1991). Direct observation of biologically-derived visual cues can be highly habitat-, locality- or species-specific, and may also have diel, seasonal and other temporal components of variability, some of which are predictable. In the most favorable circumstances objects are unlikely to be visible at distances of much more than 50 m underwater. Therefore, orientation using visual perception of the sea bottom, settlement habitat or other underwater features is likely to be possible over only tens of meters at best, and even less in turbid environments. Optical orientation also may enable larvae and postlarvae to regulate their horizontal distributions relative to the shoreline. Zooplankters migrate in the onshore-offshore direction in ponds and lakes in response to changing elevation of the shoreline (Siebeck, 1974), and it is possible that behaviorally mediated horizontal migrations occur in marine larvae. In open water away from shorelines, the light field is uniformly bright, and zooplankters do not show directional horizontal swimming. However, the elevated horizon of a shoreline produces a dark field, stimulating zooplankters to swim away from shore into deeper waters (Siebeck, 1974). This behavioral mechanism and responses to water colour has yet to be investigated in marine larvae, and it warrants examination. We would argue, however, this form or orientation is only likely to be useful on scales of tens of meters.

Orientation involving light from celestial bodies, particularly the sun and moon, requires some estimation of angle and, therefore, this form of navigation may be restricted to very shallow water. When celestial bodies (i.e., the sun or moon) vanish below the horizon a polarized light compass would be required. If orientation facilitated by lunar or solar cues is useful for navigation it would be potentially usable over vast scales. Celestial cues are spatially variable by latitude and they vary temporally on a diel, lunar and seasonal bases. Celestial cues are likely to be of limited accuracy at spatial scales below 100 km.

Light is a potentially useful cue. Most larval stages possess some form of eyes, ranging from simple light detectors to complex, image-forming organs, and these are usually present from a very early stage (Blaxter, 1975; 1986; Table 1). Fishes have an extraretinal light sense (probably involving the pineal), that in some larvae controls vertical migration (Wales, 1975). Forward (1988) called into question the results of most laboratory studies, because investigators typically used concentrated beams of white light that do not adequately simulate the diffuse filtered light in the natural underwater environment. For example, larvae of the estuarine mud crab, *Rhithropanopeus harrisii*, are positively phototactic in narrow beams of light but not under more realistic conditions (Forward and Costlow, 1974; Bentley and Sulkin, 1977). These laboratory studies indicated that larvae should occur near the surface in the daytime and deeper at night. However, the opposite response was observed in natural populations (Cronin, 1982).

Various larval stages can detect visible and ultraviolet (UV) light and distinguish colors (Bone et al., 1995; Loew et al., 1996; Losey et al., 1999; Lara, 1999; U. Siebert, pers. comm.). Forward and Cronin (1979), however, concluded that the spectral sensitivity of crab larvae is suited to the adult environment and did not change during development. We also note that sensitivity to UV may relate to protection from UV damage rather than for navigation purposes (Barcelo and Calkins, 1978). Adults and possibly larvae of some fishes can detect polarized light (Kunz and Callaghan, 1989; Flamarique and Hawryshyn, 1997; Lara, 1999). The ability to detect light levels changes with the age of presettlement forms. Fishes, for example, develop a pure cone retina shortly after hatching and rods as well as color vision (cones) do not generally develop until metamorphosis into a juvenile (Powers and Raymond, 1990).

It is clear that light intensity or changes in it are widely used for vertical distribution maintenance (Neilson and Perry, 1990). Lunar and solar cues are thought to be involved in vertical migration, especially for vertical migration for partial navigation (Manuel and O'Dor, 1997; Manuel et al., 1997). However, we endorse Forward's (1988) statement that unrealistic conditions are often used in laboratory studies.

There is some evidence that solar or lunar compasses are used by marine larvae in the way they are used by various terrestrial and freshwater animals and adult jellyfishes (Ogden and Quinn, 1984; Hamner et al., 1994). Larvae of two flatfish species can discriminate between levels of brightness of light (Blaxter, 1972), a prerequisite for detecting the azimuth of the sun, and therefore for a solar compass. Directional swimming by a damselfish (Leis, unpubl. data), and the larvae of two crab species (Shanks, 1995), both suggest that a solar compass is operational in situ. Solar compass orientation has also been claimed in juvenile grunts by Quinn and Ogden (1984). Celestial cues are used for orientation by the larvae of crabs and shrimps, and the adults of one gastropod (Table 1). We suggest that solar compass navigation has great potential where the target is huge and little accuracy is required (e.g., swimming across a continental shelf).

A view of the substratum could contribute to the maintenance of position by allowing an organism to determine displacement by currents. For example, larvae of some species normally stay very close either to the bottom or their natal reefs (e.g., Marliave, 1977; Kingsford and Choat, 1989), and at ranges of tens of meters, vision could easily play a role in such retention, at least during the day. For potential settlers, a view of the bottom would also be very informative about possible settlement habitats. Potential settlers, with image forming eyes, may also be able to determine features in the general vicinity based on shape, color, slope of the bottom or other features, such as attached vegetation. In presettlement fishes, the eye is initially strongly myopic, but acuity increases rapidly with age (Pankhurst, 1994; Shand, 1994), so it is likely that potential settlers will be able to see better and from a greater distance than younger forms. At night, we would expect that lower light levels would lead to constraints in the control of horizontal orientation (Kobayashi, 1989), as it seemingly does in some cases of vertical distribution (Leis, 1991).

Vision over tens of meters could also be important for orientation within the water column where there are sharp boundaries of turbidity or water color. Near fronts, differences of water color or turbidity should be detectable by presettlement fishes and perhaps some invertebrates. Differences in visibility may indicate different water parcels that may in themselves provide cues for orientation (e.g., olfaction).

RHEOTAXIS.—Water movement occurs at all scales from the molecular to oceanic gyres. Movements vary from essentially random (e.g., turbulence) to highly directional (e.g., the Kuroshiro Current). Many aquatic animals have the ability to detect and orient into currents (rheotaxis), and this is accomplished with the aid of a variety of senses (Montgomery et al., 1995; Montgomery et al., 1997; Table 1). However, this orientation requires a reference to determine direction of movement; otherwise, the animal has no information that it is moving.

In situations where an external reference is present, there are numerous examples of the rheotactic abilities of larval stages. For example, larval gobies returning to a stream from the sea are strongly attracted to flowing water (Smith and Smith, 1998), and this directional orientation is maintained even after the flow is cut off. Larval milkfish are rheotactic from 2 d post-hatch (Kawamura and Hara, 1980). In most situations, however, a pelagic larva has no view of the bottom and because the use of external references would be further restricted by limitations in larval visual abilities and water clarity, this approach is unlikely to be of wide use.

If there is orientation to currents by presettlement forms, without using vision (as suggested for larval crabs and lobsters, e.g., Shirley and Shirley, 1988; Cobb et al., 1989; Shanks, 1995), there are only a few options that exist for external references and there is little knowledge of their use. Directional information may be provided through sun angle or polarization of light, the detection of an ocean current moving through the earth's magnetic field and the electrical potential this produces (see 'Electrical fields'), and/or the anisotropic structure of turbulence (i.e., it has a different shape in the direction of flow than perpendicular to it). We consider the first two to be of limited use at spatial scales of less than 50 km. It is theoretically possible to detect an ocean current moving through the earth's magnetic field by the electrical potential this produces (see 'Electrical fields'), and this could enable a larva to orient. Although such ability has been proposed for an adult flatfish (Metcalfe et al., 1993), no other marine animals with a bipartite life cycle have been shown to be able to detect electrical fields. Turbulence may also provide information on the direction of flow. Since turbulence in a flow is anisotropic, it could be used for orientation and navigation.

ACCELERATION.—The use of accelerations for navigation is largely speculative. Accelerations occur primarily at a small scale associated with turbulence or, at a somewhat larger scale, with wave motion, but they might be useful in orientation at larger scales (Wang et al., 1998). Larvae of at least some species can detect accelerations, although it is unclear what senses are used. This ability may allow the detection of turbulence and wave motion. Organisms with statocysts or otoliths (e.g., fishes, cephalopods, some crustaceans) or external near-field vibration sensors (e.g., fishes, crustaceans) should be able to detect such motion: for example, blue crab megalopae respond to increases in turbulence by ascending, and to decreases in turbulence by descending (Welch et al., 1999). The ability to detect turbulence could be useful in vertical positioning or to detect the interaction of waves with shoaling bottom. Wave direction and size are not uniformly distributed. For example, near a coastline more and larger waves will come from offshore than from the direction of the coast. Waves, therefore, could provide cues about the location of shallow water or shorelines, and thus be useful in orientation at multiple spatial scales.

PRESSURE.—Pressure varies directly with depth. Therefore, a pressure sense could be useful for depth maintenance or to detect changes in tide (Rothlisberg et al., 1996). Larval sole have been found to respond to sudden increases in pressure by ascending (Macquant-Moulon et al., 1989), thus demonstrating a pressure sense. An ability to detect pressure changes is known in mollusc, crab and barnacle larvae (Table 1). In crabs, the statocysts are used to detect pressure changes as small as 0.025 atm (Wheeler and Epifanio, 1987). The responses of crabs to changes in pressure may change with developmental form and this has strong implications for transport (Sulkin, 1984) using partial navigation. A number of investigators have proposed that selective tidal stream transport would be facilitated by the ability to detect tide-induced changes in depth or current, and this has been demonstrated in a number of cases (e.g., scallops, Manuel et al., 1997), although the sense involved was not clear. Barokinesis is thought to be important for tidal stream transport in crab megalopa, but this is often confounded with other responses (e.g., responses to salinity, Forward, 1989; turbulence, Welch et al., 1999) where the relative importance of each sense is poorly known.

THIGMOTAXIS.—Thigmotaxis is used by settling invertebrates while undergoing detailed searches of the substratum (barnacles, Wethey, 1986; worms, Pawlik and Butman, 1993). In addition to searches at small spatial scales (millimeters to centimeters), positive thigmotaxis may contribute to long distance dispersal. For example, positive thigmotaxis may result in pelagic organisms associating with drifting objects (e.g., algae). A result of this latter attraction may be that the organisms will be transported with the algae. Drift of algae is strongly affected by wind direction and speed as well as currents (Kingsford, 1992; 1995). Crab megalopa, for example, associate with drift algae (Kingsford and Choat, 1985) and as a result they will be transported with the algae via currents, wind and convergences (Shanks 1983, 1985; Pineda, 1994). The resulting trajectory of the megalopa on the algae may differ considerably from that of megalopa that remain swimming in the water column. Although thigmotaxis may be important at settlement and for associating with drifting objects, this type of response does not constitute a response to environmental cues that constitutes navigation.

SENSORY RESPONSES TO MULTIPLE CUES

The use of multiple cues, and the same sense at multiple spatial scales, is common for large organisms that navigate over long and short distance, including whales (Walker et al., 1992), birds (Wiltschko and Wiltschko, 1995), turtles (Salmon and Wyeneken, 1987; Lohmann and Lohmann, 1996) and salmonid fishes (Quinn and Dittman, 1990). For larvae, the use of multiple cues and, therefore, an integrated navigational system is most likely for taxa that have multiple sense organs and low thresholds of detection of sensory information. There are examples of presettlement forms that use multiple senses. The megalopal stages of many estuarine brachyuran crabs undergo rhythmic vertical migrations which result in saltatory up-estuary transport during flood tides. Vertical migration is often based on one or a combination of responses to pressure, temperature, salinity, geotaxis, turbulence and/or light (Shirley and Shirley, 1988; Forward, 1990; Tankersley et al., 1995; Welch et al., 1999). Although the spatial scales of movement may be small, even the most primitive of metazoans (sponges) may use more than one sense. Larval sponges may be photonegative (Maldonado and Young, 1996) and then they may use chemotaxis to find an appropriate place to settle (S. Leys, pers. comm.). Research on neural pathways indicate that the detection of turbulence may be combined with chemotaxis. Male lobsters, for example, use chemotaxis to locate females at the sources of pheromonal plumes (Atema and Cowan, 1986). The plumes are characterized by turbulence that is thought to be essential for navigation. It is considered highly likely that chemotaxis is combined with mechanoreceptors that detect vibration (e.g., turbulence) because the neural pathways of these two senses are integrated in the brain (Schmidt and Ache, 1996). The receptors (pinnate sensory setae) are also found in the pueruli of lobsters and, therefore, could be used for navigation (Jeffs et al., 1997).

We have attempted to illustrate a hierarchy of stimuli that may be useful at different spatial scales (Fig. 2). Indeed, many of these stimuli are used sequentially by adult salmonids to find natal rivers (Quinn and Dittman, 1990). Given that presettlement reef fish have been demonstrated to navigate using smell on a scale of meters (Sweatman, 1983; Elliott et al., 1995) and sound at perhaps larger spatial scales (Tolimieri et al., 2000), they may use sensory hierarchies that are as complex as those used by salmon. The distinction between 'current-independent cues' and 'current-dependent cues' is useful (sensu Armsworth et al., 2000), as this dichotomy may be used to test hypotheses on the relative importance of cues to taxa of different mobility. Current-independent cues require less energy for successful attainment of the goal and, therefore, are likely to be of great importance to weak swimmers.

In conclusion, the presettlement forms of a wide range of taxa have the morphology required to detect environmental stimuli and many of them exhibit strong orientation behaviors in response to stimuli. In some cases this orientation may result in navigation to a source or partial navigation where as a result of orientation they are transported in favorable currents toward a suitable settlement site. In some cases multiple sensory responses may be exaggerated due to interpretations based only on orientation (e.g., barokinesis versus geotaxis). Multifactorial experiments (mensurative and manipulative) are required to resolve potentially confounded sensory responses. The most definitive demonstrations regarding navigation of presettlement forms has been based on responses to environmental stimuli over short spatial scales (i.e., within a few meters or centimeters of settlement sites). The morphology and locomotory abilities of many fishes and deca-

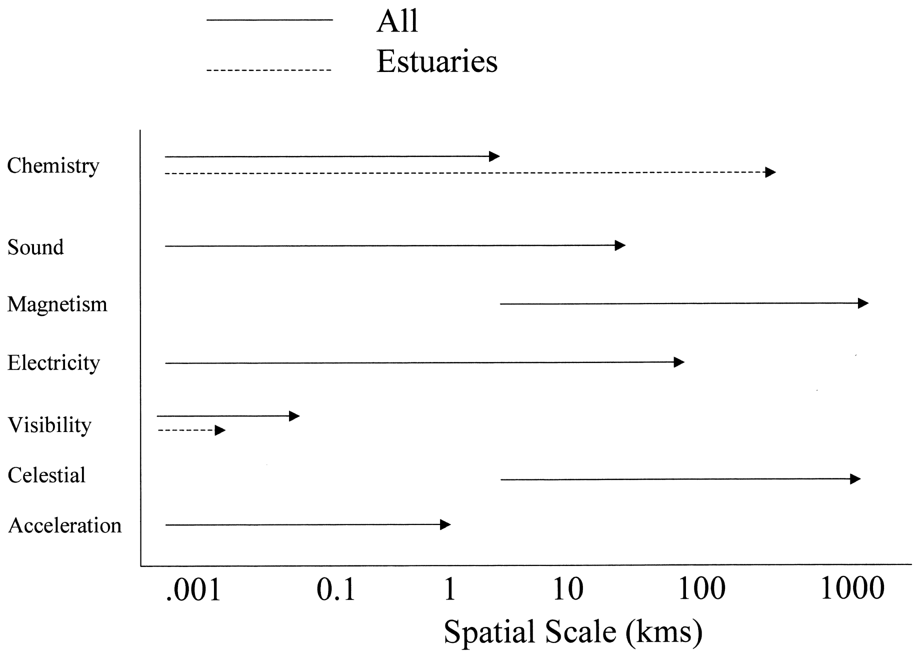

Figure 2. Relationships between sensory stimuli and the spatial scales over which they are likely to be detected (see text for sources). There will often be gradients of variation nested within a group (e.g., the chemistry of an estuarine or reefal plume may attract potential settlers, and in turn the fish or invertebrates may respond to chemistry that is specific to suitable habitat and conspecifics).

pods suggest that senses may be used to detect stimuli over much broader spatial scales (hundreds of meters to tens of kilometers). These are the spatial scales that are relevant to long distance navigation, potentially to natal environments. Presettlement invertebrates and reef fishes exhibit orientation behavior in the field (Shanks, 1995; Leis et al., 1996) and there is recent evidence that invertebrates and reef fishes (apogonids in lagoonal or oceanic waters, Atema and Kingsford, unpubl. data) orient to different water masses. A knowledge of the ability of presettlement forms to navigate will be crucial if models are to predict patterns of settlement accurately (cf Sponaugle et al., this issue). Although variation in physical transport often correlates well with patterns of settlement (e.g., invertebrates, Shanks and Wright, 1987; fish, Jenkins et al., 1997), there is often a considerable amount of unexplained variation. We suggest that some of this variation may be due to presettlement forms orienting and exhibiting choice for the timing and location of settlement. Greater research effort is required on navigation for invertebrates and fishes, and their interactions with oceanography, at spatial scales that are relevant to potential self-recruitment.

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