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Chemical cues affecting recruitment and juvenile habitat selection in marine versus freshwater systems

Stephanie M. Bilodeau · Mark E. Hay

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Abstract Marine and freshwater ecosystems differ in persistence, size, population connectivity, and the variance in physical and biotic conditions they experience. These differences may select for differing reproductive modes, life histories, dispersal strategies, and chemically cued recruitment behaviors. In marine systems, adults are commonly less mobile, while larvae spend hours to weeks to months dispersing in the plankton and may move over great distances. It is these immature larval stages that must select appropriate recruitment sites in marine environments. In freshwater systems, the fully developed adults more commonly disperse over greater distances, and it is usually adults that determine juvenile recruitment sites via their placement of larvae or fertilized eggs. Thus, in terms of large-scale habitat choices involving chemical cuing, adult stages should be selected to detect and react to habitat cues among most freshwater species, while juveniles should play this role among most marine species. Few studies assess this hypothesis, but adults of freshwater organisms as different as mosquitoes and frogs do key on chemical cues to select sites for depositing eggs or larvae, while chemical cuing of recruitment in marine systems occurs primarily among the larval stages of the numerous fishes and marine invertebrates investigated to date. Cues to general habitat features, to predators or competitors, and to specific prey or hosts have all been shown to affect recruitment. Here, we review chemically mediated recruitment in marine versus freshwater systems, summarizing what is known and suggesting unknowns that may be productive to investigate.

Keywords Chemical ecology · Settlement · Habitat selection · Larvae · Marine · Freshwater

Introduction

Marine and freshwater systems are similar in being aquatic, but they differ in size, persistence, patchiness, population connectivity, ease of large-scale dispersal, variance in physical parameters, and other features that may select for different traits involved in juvenile colonization and selection of appropriate habitats. Although the largest of lakes and freshwater inland seas approach the size, physics, and temporal stability of marine systems, most freshwater systems experience greater variance in physical regimes, patchiness of biotic interactions, and seasonality of energy and material input (e.g., due to terrestrial canopies limiting

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S. M. Bilodeau · M. E. Hay (✉)
School of Biological Sciences and Center for Microbial Dynamics and Infection, Georgia Institute of Technology, Atlanta, Georgia 30332-0230, USA
e-mail: mark.hay@biology.gatech.edu

light during the growing season, the input of terrestrial leaf-fall in the autumn, etc.). In numerous cases, a suitable freshwater habitat for developing larvae may persist for only days or weeks and not be found in the same location over time. This patchiness and variability in size and persistence also creates great variance in biotic conditions, with competitors, predators, and parasites being distributed more variably among habitat patches than likely occurs in marine systems. These differences may select for differing reproductive modes, life histories, dispersal strategies, and chemically cued behaviors between marine and freshwater organisms. Below, we compare and contrast patterns detected to date in the use of chemically cued recruitment and suggest issues that would benefit from additional investigations.

After hatching, a few larval animals in both marine and freshwater systems settle almost immediately. In contrast to this rapid settlement near the parent, most invertebrate and fish larvae in marine environments spend weeks or months in a dispersive pelagic phase where they continue to grow and develop until they are physiologically competent to settle, often remote from the parent (Pawlik 1992; Leis and McCormick 2002; Grantham et al. 2003). Larvae may travel great distances from their spawning location during this pelagic stage, but not all do so, and certain populations with dispersive larvae are surprisingly closed, with considerable self-recruitment (Leis and McCormick 2002; Almany et al. 2007; Shanks 2009; Weersing and Toonen 2009). This failure of population structure to scale with distance for numerous marine species suggests that larval behavior may be important in disrupting patterns that would be expected from physical processes alone (Cowen et al. 2006), and chemical cuing is one obvious mechanism by which larval behavior could significantly affect recruitment patterns (Gerlach et al. 2007, 2019; Dixson et al. 2011, 2014).

Most coastal and benthic marine species have complex life cycles where larvae are released into the plankton, spend minutes to months there, and then must find their way back to non-planktonic adult habitats (e.g., coastal benthic areas) to settle, metamorphose, and grow into adults (Shanks et al. 2003; Grantham et al. 2003; Shanks 2009). During this dispersal stage, larvae are in planktonic habitats that are unsuitable for post-settlement growth or survival. Marine larvae are thus commonly challenged to locate appropriate coastal sites and then appropriate sub-habitats and microhabitats into which to settle. Although they may use sounds, hydrodynamics, or other cues to help locate suitable adult habitats, portions of this search are commonly chemically mediated, especially at local scales (Pawlik 1992; Hadfield and Paul 2001; Leis et al. 2011; Lecchini et al. 2014; Dixson et al. 2014). During site selection, larvae may settle in response to chemical cues from desirable habitats, prey or hosts, and from substrate predictive of larval survivorship, but larvae also use chemical cues to avoid predators, competitors, or degraded habitats (Grossberg 1981, Krug and Manzi 1999; Pasternak et al. 2004b; Diele and Simith 2007; Dixson et al. 2014). The chemistry of settlement cues used by larvae of marine invertebrates has been reviewed by both Pawlik (1992) and Hadfield and Paul (2001).

Because many marine invertebrate species are sessile and benthic as adults (i.e., affixed to the bottom following settlement and metamorphosis—e.g., corals, barnacles, sponges, etc.), the juvenile decision of where to recruit may affect fitness as much as, or more than, any decision required of the more fully developed adult. Thus, in marine systems, this crucial decision must be made by the immature, and often only minimally mobile, larval stage. In contrast to these challenges for marine larvae, juveniles of many freshwater species either have direct development, where small adult-like juveniles are released directly into adult habitats (e.g., crayfish, live bearing fish like *Gambusia*), or have complex life cycles with aquatic juveniles and terrestrial or semi-terrestrial adults that can move across terrestrial environments to place young in patchy aquatic systems selected by the adult (e.g., aquatic insects such as mosquitoes, dragonflies, and mayflies, or toads, frogs, salamanders, etc.). Thus, in terms of large-scale habitat choices involving chemical cuing, it may be expected that adult stages will be selected to detect and react to habitat cues among many freshwater species, while juveniles will be selected to play this role in most marine species.

Larval dispersal and settlement in marine systems have been broadly studied in numerous species of fishes and invertebrates (e.g., Pawlik 1992; Hadfield and Paul 2001; Leis 2006; Hadfield 2011; Leis et al. 2011). Less attention has been given to the study of dispersal and settlement in freshwater organisms, especially with regard to the chemical ecology of site selection and other life-history transitions (Downes and Keough 1998). Marine species appear to favor dispersive larval reproductive strategies more than closely related freshwater species; freshwater species across multiple taxa more commonly employ brooding, other parental care, or dormant resting stages to cope with the localized and ephemeral nature of many freshwater environments (Hairston 1996; Vogt 2013). Although there is clear evidence of marine larvae and freshwater adults chemically assessing habitat quality for recruitment or larval deposition (Walsh 1989; Hadfield and Paul 2001; Koehl and Hadfield 2004; Schulte et al. 2011; Dixson et al. 2014; Buxton and Sperry 2017), there are few instances where the chemical cues mediating these behaviors have been identified, and relatively few investigations in general of how freshwater species may be using chemical cues to evaluate among-habitat deposition of juveniles. Below, we first address evidence of chemically mediated search for appropriate general habitats across both time and space and then the chemically mediated cuing used within these broader habitats to locate critical sub-habitats and microhabitats (e.g., specific hosts, substrate types, or safe sites from natural enemies).

Considerations for marine recruitment

While larvae released into the water column were previously considered to disperse passively at the mercy of currents and tides (Colman 1933; Yonge 1937; Pawlik 1992; Downes and Keough 1998; Leis 2018), more recent studies suggest that marine larvae may use poorly understood behaviors to stay close to parental environments even when spending weeks developing in the plankton (Almany et al. 2007). There is growing evidence that this surprising control of location by small, less mobile larvae despite currents that should disperse them far from parental locations may be chemically mediated (Gerlach et al. 2007). To recruit to appropriate settlement sites, larvae may rely on a hierarchy of physical and chemical cues that may change with distance from the eventual recruitment site—using light, geomagnetic cues, or sound to navigate to coastal settings and then chemical cues to select among those coastal sites (Le Tourneux and Bourget 1988; Gerlach et al. 2007; Lohmann et al. 2008; Lecchini et al. 2014; Dixson et al. 2014; Gordon et al. 2018). Larvae from at least one coral reef fish can detect chemical cues associated with a healthy reef up to 1 km away, although the chemical compounds themselves may disperse farther (Lecchini et al. 2014). Relatively little is known about the outer limits of chemosensory detection in larval marine organisms. Numerous marine larvae can orient based on geomagnetic cues and sounds of coastal systems across distances where chemical cues may be ineffective (Lohmann et al. 2008; Cresci et al. 2017; Gordon et al. 2018). Additionally, once near shore, multiple cues may be required to assure recruitment to appropriate habitats; as an example, chemical cues may be acted on more strongly if appropriate flow cues are also present (Pasternak et al. 2004b; Gaylord et al. 2013). Settlement behavior may be activated by hierarchical and multimodal cues or triggers, both before (Pasternak et al. 2004b; Wheeler et al. 2016) and after competence is achieved (Boudreau et al. 1993; Davis and Stoner 1994; Lambert and Todd 1994; Morello and Yund 2016).

Given the overwhelming effect of settlement site selection on the fitness of sessile benthic species (Connell 1961; Olson 1985; Toth et al. 2015; Beatty et al. 2018), it may be reasonable to think of a series of cues that act like a "combination lock" (with each occurring in sequence) to initiate successful settlement. A larva may need to receive the sounds and hydrodynamic cues of being near shore and over a healthy reef, then a chemical cue of the general environment being receptive to larvae that activates a swim-down and explore behavior, and finally, a contact chemical, textural, or light, etc., cue that the appropriate microsite for attachment has been found (Leis and McCormick 2002). As a possible example, larvae of the sea urchin *Strongylocentrotus purpuratus* respond to turbulent shear typical of suitable coastline habitat by becoming competent to settle and therefore receptive to chemical cues associated with settlement (Gaylord et al. 2013). If a complex series of cues must be encountered to induce settlement, then simple laboratory or single cue experiments may produce variable outcomes or be context dependent. However, it is comforting that numerous simple experiments have produced robust results regarding organismal responses to various chemical cues (e.g., Pawlik and Hadfield 1990; Boudreau et al. 1993; Munday et al. 2009; Dixson et al. 2014).

Larvae of the southern rock lobster *Jasus edwardsii* show attraction to coastal water, relative to oceanic water, suggesting that chemical cues are important in guiding their navigation from pelagic to coastal systems and settlement in these environments (Hinojosa et al. 2018). Numerous reef fishes cue on compounds or chemical mixtures released by terrestrial vegetation to navigate toward coastal reefs (Dixson et al. 2008, 2011; Brooker et al. 2020). Clown fish that live in anemones occurring on fringing reefs adjacent to terrestrial habitats are attracted to chemicals released by coastal terrestrial vegetation and may be able to use cues from leaves drifting from islands to "follow the trail" to coastal sites with anemones (Dixson et al. 2008). However, these juvenile fish are repelled by the cues of vegetation types that would not normally be encountered near island shorelines (Dixson et al. 2008). Reef fishes are also attracted by cues from fallen leaves of coastal mangroves, but more by water conditioned with mangrove leaves collected from sites remote from human settlements than by water conditioned with leaves from mangroves located near humans (Brooker et al. 2020). In neither of these instances are the compounds producing these behaviors known, but both indicate that human presence, agricultural activities, or alteration of native coastal vegetation may suppress the resilience of coastal fish populations due to disrupting chemical cues used by recruiting larval fishes.

Once larval stages of fishes and corals near the coast, they also make decisions on whether to recruit and settle or keep drifting in hopes of finding better habitats based on chemical cues from abundant corals on healthy reefs versus cues from abundant macroalgae on degraded reefs (Lecchini et al. 2013; Dixson et al. 2014; Brooker et al. 2016). As an example, cues from coral-rich and macroalgae-poor marine-protected areas (MPAs) are attractive to juvenile fishes and coral larvae (Lecchini et al. 2013; Dixson et al. 2014). In contrast, cues from coral-depauperate and macroalgae-rich fished areas are repellant to both juvenile fishes and larval corals. Additionally, both fishes and corals make nuanced choices based on cues from specific species of corals and macroalgae. Both avoid cues from macroalgae that predictably bloom on degraded reefs more than cues from macroalgal species that commonly occur in low abundance on both healthy and degraded reefs (Dixson et al. 2014).

Fishes are more attracted to cues from corals that are most strongly suppressed by physical and biotic disturbances and are less attracted to corals that are resilient to such disturbances (Dixson et al. 2014). This is presumably due to the most sensitive corals being more honest cues to reef health and resistant corals providing less information. Coral larvae are more attracted to cues from conspecific corals than heterospecific corals, but also more attracted to diverse mixes of corals than to cues from conspecific corals alone (Dixson et al. 2014). When water-holding cues from coral-rich MPAs and macroalgal-rich fished areas are mixed at various ratios and tested for their attractiveness to four species of reef fishes, most species start avoiding the ratio that would represent a macroalgal cover of a bit over 10% on natural reefs (Brooker et al. 2016), suggesting a critical level of macroalgal cover which managers should try to avoid as a way to prevent generating chemical cues that suppress fish recruitment and thus reef resilience.

Considerations for freshwater recruitment

Most juveniles of freshwater species do not drift in the plankton, but rather: (1) are taken to recruitment habitats by parents and deposited there as eggs or larvae, (2) persist as resting stages in sediments during unsuitable periods (e.g., droughts when water bodies dry out, etc.), or (3) may be dispersed by winds or by adhering to larger animals (waterfowl, etc.) that move among patches of aquatic habitats. Given this, we might not anticipate strong selection for chemical cuing to habitat types by the larvae of freshwater species that occur in small isolated freshwater systems (pools and ponds). However, mobile, terrestrial parents (e.g., insects, amphibians) moving among habitat patches and choosing patches into which they deposit juveniles might be selected to chemically assess these habitats for threats that would suppress the survivorship or growth of their larvae before depositing them there (Buxton and Sperry 2017). In contrast to small ponds or ephemeral pools, large inland seas approach the size of oceans, and species in these systems may experience selection for detecting coastal versus pelagic systems that are similar to those experienced by marine species. Juvenile and larval fishes that use nearshore environments in the Laurentian Great Lakes can distinguish between nearshore and offshore water, likely using chemical cues to orient and navigate to nearshore habitats (Malinich and Pangle 2018). Additionally, for species using streams and rivers, there must be dispersal mechanisms allowing upstream migration so as to prevent population wash-out from headwaters. Adults dispersing back upstream for juvenile deposition is one mechanism allowing this (Williams and Hynes 1976; Müller 1982).

Evidence for chemical sensing of habitat quality by adults that are depositing larvae or that are dispersing upstream is not extensive but comes from groups as different as frogs and mosquitoes. The poison frog *Ranitomeya variabilis* deposits its eggs in water-filled plant cavities, with males then moving embryos among cavities as required by changing conditions. Tadpoles of this species prey on other tadpoles, and parental frogs favor cavities containing heterospecific, non-cannibalistic, tadpoles upon which their young can feed, while they avoid cavities with cues of conspecifics or other cannibalistic species (Schulte et al. 2011; Buxton and Sperry 2017). Buxton and Sperry (2017) review how anurans use chemical cues to detect predators or competitors and decide where to deposit eggs and tadpoles. Similarly, multiple species of adult mosquitos appear to use undescribed chemical cues to lessen deposition of their young in waters containing larval predators or potential competitors (Chesson 1984; Stav et al. 1999; Eitam and Blaustein 2004; Blaustein et al. 2004, 2005; Arav and Blaustein 2006; Munga et al. 2006; Segev et al. 2017) and may also avoid depositing eggs in pools already occupied by cannibalistic larvae of conspecifics (McCrae 1984; Koenraadt and Takken 2003). For at least one species of mosquito and its larval predator, a chemical cue involved in selective oviposition decisions appears to be air-borne and does not require the adult to contact the water to detect it (Silberbush and Blaustein 2008). Flies (Diptera) also avoid oviposition in bromeliad pools with a caged predator (carnivorous mosquito larva). Some families of Diptera also extend this avoidance to predator-free pools in close proximity to the predator pool (risk contagion), while other families instead colonize these predator-free pools in greater numbers, likely due to habitat compression from the predators (Turner et al. 2020). Predator detection by the flies is likely to be chemical, although no specific cues were isolated and identified.

Complex life cycles and between habitat transitions

With the exception of a few crustaceans, most marine species are fully marine or shift between marine and lower salinity waters throughout their lives. In contrast, numerous freshwater organisms shift between aquatic and terrestrial environments at different developmental stages. This shift occurs for many insects, numerous amphibians, and several reptiles and crustaceans and is commonly associated with dramatic morphological and behavioral changes over the lifetime of these organisms. As an example, the newt *Notophthalmus viridescens* lives as an aquatic larva early in life shifts to terrestrial living in the red eft juvenile stage lasting for a few years and then re-enters aquatic life as an adult (Roe and Grayson 2008). The mid-life terrestrial stage allows potential dispersal to other water bodies and may allow population connection among different patches of aquatic habitats (Gill 1978); toads and frogs also transition from aquatic tadpoles as juveniles to terrestrial or semi-terrestrial adults. Similarly, many insects spend much of their lives as aquatic juveniles but then emerge, disperse, and mate as (often short-lived) terrestrial adults that then deposit juveniles back into aquatic environments (Merritt and Cummins 1996; Cayrou and Céréghino 2005; Lancaster and Downes 2013). More mobile adults can disperse zygotes back to head waters in riverine systems or among lakes, ponds, or puddles, choosing the most appropriate habitats into which to deposit their juveniles (Müller 1982; Uno and Power 2015). Mosquitoes, mayflies, dragonflies, and many other insects would be examples (Lancaster and Downes 2013), as would a few species of marine crabs that live on land as adults but must release their young into the sea where they disperse and develop in the plankton before returning to land (Burggren et al. 1988; Anger 1995).

A small number of marine insects that have lengthy submerged larval stages and short terrestrial adult lifespans might be expected to follow similar chemical cues to those employed by freshwater insects. For example, the marine midge *Clunio marinus* emerges as an adult to mate and oviposit during a short window of mere hours determined by the availability of exposed substrate at low tide (Missbach et al. 2020). This is reminiscent of the short adult lives of mayflies and other freshwater insects. However, no chemical cues associated with oviposition selection in this marine insect have been identified. In fact, *C. marinus* adults have reduced olfactory systems compared to their larvae and to adults of other dipteran species (Missbach et al. 2020).

Aquatic species with diverse diadromous life histories may rely on complex chemical cues to guide their travel between salt and freshwater environments (or vice versa). These include anadromous fishes like salmon and sea lampreys, whose marine adults return to freshwater to breed, as well as amphidromous species like gobies that may travel between freshwater and salt water at different life stages for purposes other than reproduction. The chemical indicators these species rely on may be paired with magnetic or hydrodynamic cues used to navigate in the open ocean (Endres et al. 2016; Cresci et al. 2017). Various species of salmon appear to rely on chemical cues to return to their natal stream for reproduction (Groves et al. 1968; Groot and Margolis 1991). The juveniles of these fish undergo chemical imprinting that allows them to navigate back to the same freshwater location where they hatched after years at sea. When not interrupted by fisheries or other human activities, this remarkable chemical homing behavior on the part of adults has the effect of maintaining genetically and behaviorally distinct populations of salmon despite their close spatial proximity (Schindler et al. 2010; Prince et al. 2017). Similar chemical imprinting also may occur in larval coral reef fishes (Gerlach et al. 2019), which could be one method by which seemingly open marine populations of fishes may in fact achieve high levels of self-recruitment (Almany et al. 2007). Anadromous sea lampreys (*Petromyzon marinus*) utilize conspecific pheromone cues when migrating upriver to spawn (Hogg et al. 2013), specifically responding to a fatty-acid-derived pheromone ((+)-(2S,3S,5R)-tetrahydro-3-hydroxy-5-[(1R)-1-hydroxyhexyl]-2-furanoctanoic acid; Fig. 1 compound 1) from larvae to determine suitable spawning areas, rather than returning to their own natal streams (Waldman et al. 2008; Li et al. 2018).

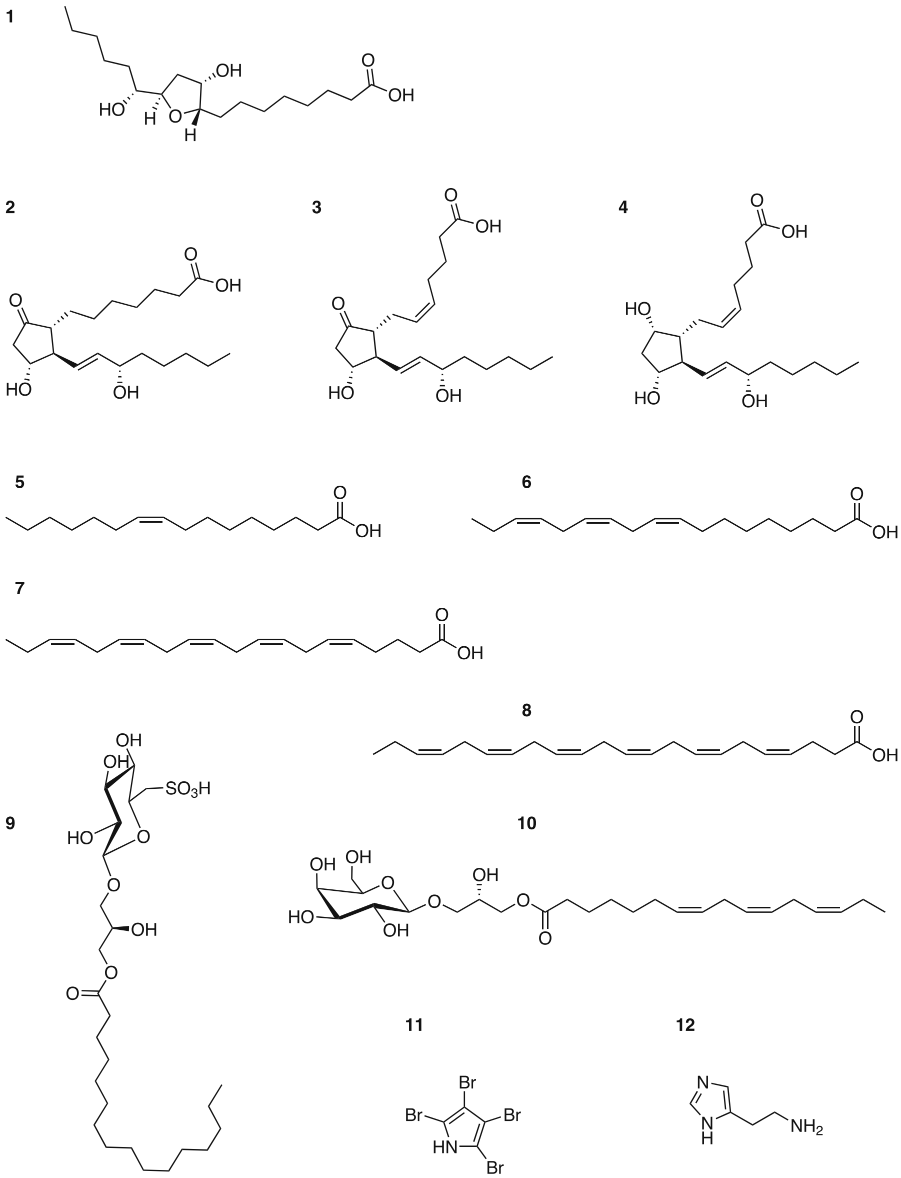
While some well-known species like salmon and eels move between marine and freshwater systems but spend much of their life in marine environments, the reverse also occurs. Multiple freshwater or brackish water shrimps and crabs “export” larvae to more saline environments for hatching and early development. These crustaceans often need sufficiently high salinity to hatch or metamorphose, possibly an evolutionary remnant from a fully marine ancestor. After hatching, the post-larval juveniles migrate upstream to return to adult habitat, following hydrodynamic or conspecific chemical cues (Anger et al. 2006; Bauer 2011). Multiple Hawaiian species of gobies (small benthic fishes) climb waterfalls as juveniles in order to return to upstream adult habitat after being swept out to sea when hatching. The goby *Sicyopterus stimpsoni* uses chemical cues from stream water to initiate waterfall climbing behavior as a migrating juvenile. *S. stimpsoni* leaves a mucous trail as it climbs; this could contain chemical cues for conspecifics, although the ability of other gobies to follow the trail appears weak (Leonard et al. 2012). These gobies, like many diadromous animals, appear to follow a more marine-typical pattern of larval or juvenile dispersal and habitat selection, rather than the adult selection of egg or juvenile location seen in many fully freshwater species.

Contrasts within taxonomic groups that occur in both systems

Contrasting reproductive and chemical cuing strategies of freshwater insects and amphibians with those of marine fishes and invertebrates risks confounding differences due to lineage with differences due to freshwater versus marine systems. However, several groups occur in both systems and allow a contrast less confounded by taxonomy (crustaceans, fishes, etc.). Taxonomic groups that occur in both marine and freshwater systems commonly have divergent systems of reproduction, dispersal, and habitat selection. Marine species of many taxa appear to favor dispersive larval reproductive strategies more than related freshwater species, which may instead employ direct development, extended parental care, or dormant resting stages to cope with the ephemeral nature, spatial patchiness, and smaller size of most freshwater environments (Hairston 1996; Balian et al. 2008; Vogt 2013). In most cases, little is known about the specific compounds or mixtures responsible for these chemically cued behaviors and strategies.

Comparison of freshwater and saltwater crustaceans suggests that freshwater crustaceans show more instances of brooding and caring for offspring than related marine species (Vogt 2013). Although some marine crustaceans provide varying degrees of

Fig. 1 Structures of attractor and inducer compounds described in the text



parental care to eggs prior to hatching (Cobb et al. 1997), they are all characterized by a dispersive larval phase that forces juveniles to make their own settlement and habitat selection decisions. Multiple species of marine shrimps, lobsters, crabs, and barnacles produce dispersive pelagic larvae that may utilize complex cues and behaviors to recognize suitable habitat and previously recruited conspecifics during settlement (Boudreau et al. 1993; Pasternak et al. 2004a, 2004b; Goldstein and Butler 2009; Hinojosa et al. 2018). In contrast, juveniles of freshwater crayfish (Little 1975, 1976), certain freshwater shrimps (Rodríguez and Cuesta 2011), and freshwater crabs (Anger 1995; Cumberlidge 1999) are hatched and kept close by their parents until they are sufficiently grown. Freshwater crayfish maintain contact with their offspring from hatching through multiple larval instars, providing protection and parental care until the juveniles are large enough to fend for themselves and disperse from the immediate location of the parent. Crayfish larvae rely on chemical cues to maintain contact with parents during their brooded early stages (Little 1975, 1976). In a freshwater shrimp, both larvae and brooding mothers respond to waterborne predator cues with changes in development or morphology of the larvae and body mass of adults (Ituarte et al. 2014). Therefore, parental care does not appear to preclude the possibility of brooded larvae detecting and responding to environmental cues, much as independently settling larvae might.

Despite the largely consistent crustacean pattern of larval dispersal in marine systems and brooding in freshwater systems, adult care for juveniles is not exclusively a freshwater trait. As an example, in response to predators, adult marine urchins release a chemical cue that attracts juveniles to shelter under adults (Nishizaki and Ackerman 2005). This is operationally similar to the cue used by late-instar, juvenile crayfish to relocate their mother for shelter after foraging.

For freshwater fishes, virtually all are demersal spawners that produce relatively few large eggs; in contrast, most marine fishes are pelagic spawners producing large numbers of small eggs (Duarte and Alcaraz 1989). The larvae of freshwater fishes are 10 × larger at hatching, have lower metabolic rates, and spend shorter times in larval stages than do marine fishes; their larger size is correlated with a 44 × increase in larval survival for freshwater versus marine fish larvae (Houde 1994), suggesting more parental investment per juvenile by freshwater fishes (as is the case for freshwater crustaceans). The shortened larval duration and smaller size of numerous freshwater habitats suggest that fishes in freshwater environments may experience less selection for chemically cued settlement than do marine species, but this has not been assessed.

Chemical cuing of recruitment in time

Both marine and freshwater species may avoid periods of physiological or biological stresses by adopting resting stages that persist in sites safe from these stresses (in bottom sediments, in cracks and crevices, or other micro-refuges) or that act like a seed bank to spur succession and regrow the population or community when more favorable conditions return (Hairston 1996; Pinceel et al. 2018). Given the more temporally variable nature of freshwater systems, one might expect greater selection for short-lived, rapidly maturing adults that produce long-lived resting stages (years to decades) in freshwater than in marine systems, and this is the case for multiple invertebrate taxa (Hairston and Cáceres 1996). These dormant stages are dispersing in time instead of space, resisting suboptimal conditions and emerging later in response to a variety of cues, some of them chemical. Some rotifers and crustaceans produce cysts or eggs that remain viable for decades (Hairston and Caceres 1996; García-Roger et al. 2005). Marine copepods and freshwater rotifers are notable for their use of dormant propagules, although many other taxa, including sponges, bryozoans, cnidarians, and flatworms, also employ some form of dormancy or delayed hatching in response to certain environmental conditions. These dormant resting stages may also include features like spines to aid in overland dispersal by attaching to carrier species, and these morphologies are more common in freshwater species than in marine members of these same taxa (Pronzato and Manconi 1994; Jankowski et al. 2008; Massard and Geimer 2008; Schockaert et al. 2008).

Chemical cues in the environment, as well as physical cues (e.g., temperature and light), can be important in mediating hatching. Eggs of euryhaline rotifer *Brachionus plicatilis* hatch in response to hydrogen peroxide and three different prostaglandins (Fig. 1 compounds 2–4) that are likely produced from the oxidation of unsaturated fatty acids in the eggs (Hagiwara et al. 1995). Snell (1998) reviews the chemical ecology of rotifers. Eggs of the salamander *Ambystoma babouri*s can delay hatching in response to chemical cues from sunfish predators (Moore et al. 1996), and dormant cysts of the freshwater dinoflagellates *Ceratium hirundinella* and *Peridinium aciculiferum* hatch not only in response to temperature, but also hatch with less frequency in the presence of exudates from predatory zooplankton (Rengefors et al. 1998). The marine dinoflagellate *Alexandrium ostenfeldii* forms similar but temporary (< 8 h) cysts in response to chemical cues from conspecifics infected with lethal parasites (Toth et al. 2004). Hatching (or delay thereof) in response to chemical cues is clearly not limited to either freshwater or marine environments. However, given the frequent drying and wetting of temporary pools in numerous freshwater settings and that pool age or location may result in patchiness of natural enemies, one might expect greater selection for resting stages to be able to chemically detect the presence of consumers or other enemies and delay or speed hatching accordingly in such freshwater habitats than in more stable and connected marine systems. We could find no rigorous assessment of this hypothesis, but it seems worthy of attention.

Within-habitat chemical cues and signals

Predator and competitor cues

Multiple species of larval anemone fishes (Dixson et al. 2010, 2012; Munday et al. 2016), megalopae of marine crabs (Welch et al. 1997; Banks and Dinnel 2000; Tapia-Lewin and Pardo 2014), oyster larvae (Pruett and Weissburg 2019), and barnacle larvae (Johnson and Strathmann 1989; Ellrich et al. 2016) detect and avoid chemical cues of predators during settlement. The presence of predator cues pre- and post-settlement may also alter growth and development of marine invertebrates (Manríquez et al. 2013; Bjærke et al. 2014; Pruett and Weissburg 2019), either through reallocation of resources toward defensive traits like thicker shells or by increasing growth directly, presumably to increase the possibility of escaping in size from these predators. Relyea (2001, 2007) reviews how predators similarly affect the growth, development, and behavior of freshwater larval anurans, and larvae more generally.

Larval and early juvenile marine fishes of multiple species may learn to associate chemical cues from injured conspecifics (indicative of predation) with previously unfamiliar predator cues and then avoid chemical cues associated with those predators thereafter (Larson and McCormick 2005; Mitchell et al. 2011a, 2011b; Ferrari et al. 2012). This learning response could allow settling larvae to assess potential habitat more quickly and accurately, even when unfamiliar with local predators, improving survival during and immediately following recruitment. Green frog tadpoles similarly respond to predator chemical cues with spatial avoidance behaviors only when those predator cues are paired with alarm cues from a captured conspecific (Brown et al. 2019). Tadpoles may also rely on chemical cues from consumed conspecifics to respond to an invasive predator, even when they do not require these additional cues to respond appropriately to a native predator (Nunes et al. 2013).

Chemical detection of enemies can even occur pre-hatching. Marine fishes and freshwater amphibians and crustaceans can learn chemical cues from their environment while still in the egg and respond appropriately upon hatching through changes in both behavior and development. Cues from predation on both conspecifics and heterospecifics altered embryonic development in a freshwater shrimp (Ituarte et al. 2019). Predator cues combined with cues from injured conspecifics triggered bullfrog embryos to develop into larger larvae that might better survive in a predator-rich environment and to exhibit increased use of refuges from predators when the perceived level of predation risk changed between the cues detected as embryos and those detected as larvae (Garcia et al. 2017). Gray treefrog tadpoles that had already hatched similarly grew faster and were more likely to develop into a stronger swimming morph when exposed to predator-associated cues (McCollum and Leimberger 1997), although not all amphibian larvae respond this way (Anderson and Petranka 2003).

Marine damselfish embryos can learn to associate predator chemical cues with the threat of predation based on cues to which they are exposed while still in the egg. After exposure to predator cues in combination with conspecific chemical alarm cues, the embryonic damselfish exhibited increased heart rate, which is associated with antipredator behavior, in the presence of predator cues (Atherton and McCormick 2015). There is some evidence that auditory cues may have similar effects on this same damselfish and related species as embryos (Jain-Schlaepfer et al. 2018; Fakan and McCormick 2019). Embryonic clownfishes gain the ability to respond to auditory cues three days post-fertilization, and this ability to detect sound develops further over the next six days (Simpson et al. 2005). These behavioral studies show that embryos can detect and respond to auditory and chemical cues even in early stages of development. Thus, embryonic animals in aquatic systems can detect chemical, and possibly other, cues to environmental risks and respond behaviorally and developmentally in ways that enhances their fitness when they hatch and emerge as larvae.

Larvae of some marine ascidians detect the species and densities of settled larvae of other ascidians (presumably due to chemical cues) and avoid settling on substrates with high densities of species that are better competitors while not avoiding equivalent densities of species that are inferior competitors (Grosberg 1981). In a similar case of a competitor mediating settlement of another species, the polychaete worm *Thelepus crispus* contaminates sediments around its burrow with a long-lasting, localized brominated aromatic compound, 3,5-dibromo-4-hydroxy benzyl alcohol (Fig. 2 compound 13), which causes the polychaete *Nereis vexillosa* to avoid that area during recruitment (Woodin et al. 1993). Competitor avoidance (or lack thereof) by settling marine larvae appears species-specific (Young and Chia 1981; Grosberg 1981; Petersen 1984; Bullard et al. 2004; Bouchemousse et al. 2017) and likely depends on the relative competitive abilities of the larva in question. Larvae of certain corals will avoid settling on macroalgae (Olsen et al. 2016) or on surfaces contacted by algae (Campbell et al. 2017), although some coral species are more discerning than others and may be expected to fare better on algae-dominated reefs if they are able to detect and avoid settling on or near macroalgal competitors (Olsen et al. 2016).

Conspecific cues

Larvae or juveniles of species that settle gregariously often experience greater intraspecific competition but benefit from indications of site suitability, proximity to future mates, and possibly increased survival due to “safety in numbers.” The barnacles *Elminius modestus* and *E. covertus* settle in response to both hydrodynamic and chemical cues from conspecific adults (Wright and Boxshall 1999). Settlement in the barnacle *Amphibalanus amphitrite* and related species is induced by both an unidentified waterborne cue (Elbourne and Clare 2010) and a settlement-inducing protein complex (SIPC), that is a large glycoprotein of known structure (Matsumura et al. 1998) with both attractive and aversive domains that result in density-dependent effects on settlement (Kotsiri et al. 2018). Gregarious settlement is adaptive for species like barnacles that are sessile, internal fertilizers that need close proximity for mating. Planktonic larvae of the marine slipper shell *Crepidula fornicata* also settle gregariously and often near conspecific adults (Cahill 2015), with settlement being mediated by an abiotic cue (KCl), multiple chemical cues based on unknown compounds that appear to be associated with conspecifics (Cahill and Koury 2016), and/or dibromomethane (DBM), which is produced by co-occurring red algae (Taris et al. 2010).

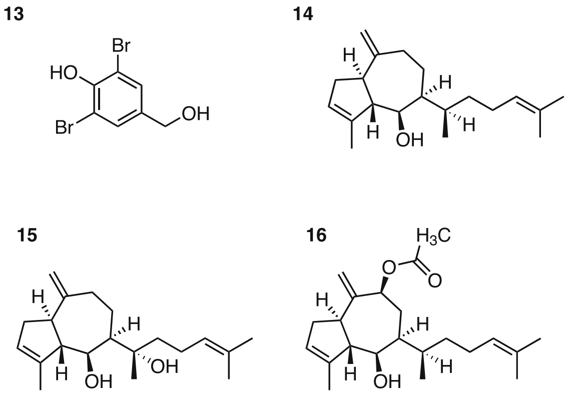


Fig. 2 Structures of aversive compounds described in the text

Adult conspecifics can serve as indicators of suitable habitat for settling larvae. Multiple oyster species settle gregariously in response to chemical cues that may be associated with adult conspecifics (Tamburri et al. 2008), and if deprived of appropriate settlement cues, larval oysters, as well as other marine invertebrates, eventually become more willing to settle with age, supporting the “desperate larva” concept (Meyer et al. 2018). Larvae of the solitary ascidian *Pyura chilensis* are attracted to adult conspecifics, in combination with other habitat cues, and settle gregariously in suitable microhabitat areas (Manríquez and Castilla 2007). Numerous crab megalopae are also induced to settle and metamorphose due to chemical cues from adult conspecifics, as well as other habitat cues (O’Connor and Gregg 1998; O’Connor and Judge 1999; Diele and Simith 2007; Anderson and Epifanio 2009; Simith et al. 2017). Planktonic polychaete larvae of a reef-building species settle and metamorphose in the presence of specific free fatty acids (FFA) from the sand matrix of adult tubes. FFA molecules that induce settlement all share certain structural features, suggesting receptor specificity, and include palmitoleic acid, linolenic acid, eicosapentaenoic acid, and docosahexaenoic acid (Fig. 1 compounds 5–8), in order of decreasing effectiveness (Pawlik and Faulkner 1986). Similar results were obtained for a related polychaete species (possibly subspecies) from a different geographic region (Pawlik 1988).

Young-of-year lobsters settle at higher densities in the presence of older juvenile lobsters, despite potential for increased competition or predation (Burdett-

Coutts et al. 2014). Larvae of the coral reef wrasse *Thalassoma hardwicke* initially settle in benthic macroalgae using visual cues, but following metamorphosis, they are then attracted via chemical and visual cues to coral colonies occupied by conspecifics (Lecchini et al. 2007). Young animals may also use chemical cues to avoid closely related individuals. Recently hatched softshell turtles (*Apalone spinifera*) detect chemical cues from conspecifics after hatching. They are attracted to conspecific cues over cues from heterospecifics, and they prefer the cues of unrelated conspecifics to those of relatives from the same clutch (Whitear et al. 2016).

Host finding

Chemical cues aid larvae of specialist species in identifying prey or hosts and, for some species, initiate physiological changes as part of the settlement process. Multiple species of sea slugs begin metamorphosis in response to chemical cues from specific corals, bryozoans, or algae upon which they specialize or feed preferentially (Pires and Hadfield 1993; Lambert and Todd 1994; Krug and Manzi 1999; Botello and Krug 2006). *Phestilla sibogae* larvae drifting above a reef sink in response to a chemical "inducer" from their preferred coral prey; if the cue does not lead to host contact, they resume swimming when the cue is lost (Koehl et al. 2007). This cue induces settlement and metamorphosis and is necessary for their ability to attach to surfaces and withstand turbulence that might dislodge them (Koehl and Hadfield 2004). In some cases, hydrodynamics may be necessary for the accurate detection of host chemical cues, as with larvae of the symbiotic barnacle *Trevathana dentata* that rely on "odor-gated rheotaxis," a combination of initial chemical cue detection and orientation in flow, to locate their coral hosts (Pasternak et al. 2004b). However, another barnacle species, *Heterosaccus dollfusi,* that parasitizes the crab *Charybdis longicollis* can locate its host either with or without flow by utilizing chemotaxis, sometimes combined with rheotaxis (Pasternak et al. 2004a), possibly an adaptation to the more mobile nature of this host species and the likelihood of encountering *C. longicollis* in both high-flow and low-flow (or no) environments. Larvae of marine bryozoan *Membranipora membranacea* appear to use chemical cues to identify their preferred algal substrate for settlement and to respond with different behaviors when contacting their preferred host or another alga in flow (Matson et al. 2010). Anemonefish larva uses waterborne chemical cues to identify and move to host anemone species in preference to other anemones and choose healthy hosts over bleached anemones (Scott and Dixson 2016).

Many freshwater insect larvae also have specific hosts, notably sponges and bryozoans. However, it remains unclear to what degree adults of these species with specific larval hosts or food sources can detect the hosts when depositing eggs in surface waters. Thus, larval habitat selection could take place after hatching in response to a range of cues, or adult insects might use chemical cues to predetermine that they are placing eggs into waters containing the prey of their larvae. Given the many examples of freshwater insect larvae that live in and/or feed on sponges (Corallini and Gaino 2003; Fusari et al. 2012, 2014; Rothfuss and Heilveil 2018), including many specialists, this would be a productive area for investigation.

Cues from specific substrates or microbial biofilms

Benthic organisms and the microbes that occupy their surfaces can produce compounds that stimulate or repel settling larvae. Crustose coralline algae (CCA) commonly serve as settling sites for a variety of marine benthic invertebrates including hard and soft corals (Slattery et al. 1999; Heyward and Negri 1999; Harrington et al. 2004). In Australia, coral larvae preferentially settle on certain species of CCA while avoiding others; their preferences are correlated with both post-settlement survivorship and with attraction to chemical extracts from the different species of CCA (Harrington et al. 2004). Avoided species of CCA periodically slough their upper layers, causing larval coral mortality due to detachment. It has been argued that microbes associated with CCA, or microbial biofilms in general, produce the chemical cues attractive to settling corals (Negri et al. 2001; Webster et al. 2004). Tetrabromopyrrole (TBP; Fig. 1 compound 11), a compound isolated from *Pseudoalteromonas* bacteria, was shown to induce settlement in *Acropora millepora* and related corals (Tebben et al. 2011, 2015). However, Tebben et al. (2015) suggest that algal compounds (2R)-1-O- (palmitoyl)-3-O-α-D-(6'-sulfoquinovosyl)-sn-glycerol and (2S)-1-O-(7Z,10Z,13Z-hexadecatrienoyl)-3-O-β-Dgalactopyranosyl-sn-glycerol (Fig. 1 compounds 9 and 10) in the CCA stimulate greater settlement of coral larvae than CCA-associated bacterial biofilms, without inducing potentially fatal metamorphosis without attachment, which occurs in response to TBP alone. There is no logical imperative that both, or either, mechanism cannot be active for different settling larvae or different species of CCA.

Sea urchin larvae may be induced to settle and metamorphose in response to specific bacterial biofilms associated with coralline algae (Huggett et al. 2006). Multiple sponge species also appear to use CCA and their associated chemical cues, as well as cnidarian GLW-amide neuropeptides, as settlement cues, suggesting that larvae from multiple phyla may share similar signal transduction pathways for settlement and metamorphosis onto these predictable substrates that are omnipresent in marine systems (Whalan et al. 2012).

Substrate-based cues may be contact-based or discernable from a distance. The red alga *Delisea pulchra* produces a water-soluble compound that induces settlement and metamorphosis in Australian sea urchin larvae that settle preferentially on this alga. This compound was previously identified as a floridoside–isethionic acid complex (Williamson et al. 2000), but that identification was later corrected to histamine (Fig. 1, compound 12) (Swanson et al. 2004). Histamine has since been shown to induce metamorphosis in other urchin species as well (Swanson et al. 2012), with organisms that produce more histamine generally inducing greater urchin settlement (Swanson et al. 2006).

Shipworms of the family Teredinidae appear to use waterborne cues to identify suitable wood substrate after making initial contact (Toth et al. 2015). Various marine wood-boring invertebrates may also rely on chemical cues indicative of previous attacks by conspecifics (shipworms; Gara et al. 1997), conspecific presence (bivalves; Voight 2007), tree bark (shipworms; Gara et al. 1997), and microorganisms (isopods; Boyle and Mitchell 1981; Cragg et al. 1999) when choosing a substrate during larval settlement.

Larvae of the colonial ascidian *Diplosoma similis* show selectivity among surfaces prior to contact, allowing avoidance of potential predators and preferential selection of desirable substrates that are relatively rare. This behavior likely results from chemical cues, but this was not directly assessed (Stoner 1994). Larvae of the barnacle *Balanus improvisus* avoid settling on or near the sponge *Halichondria panicea*; the sponge appears to release a water-soluble compound that deters settlers pre-contact (Toth and Lindeborg 2008). The alga *Dictyota menstrualis* produces diterpene alcohols that both prevent fouling organisms from colonizing the alga's surface and deter herbivore feeding (Schmitt et al. 1995). Larvae of the bryozoan *Bugula neritina* failed to settle on *D. menstrualis* after contact with its surface, but settled readily on the surface of a preferred host alga. Substrates treated with surface rubbings from *Dictyota* were rejected by *B. neritina* larvae, as were substrates treated with various pure diterpene alcohols from this algal genus. When *B. neritina* larvae were forced to settle on substrates coated with the diterpene alcohols produced by co-occurring species of *Dictyota* (pachydictyol A, dictyol E, and dictyol B acetate; Fig. 2 compounds 14–16), all compounds caused larval mortality and abnormal development, with effects increasing as a function of compound concentration (Schmitt et al. 1995, 1998).

Larvae of the sessile freshwater rotifer *Collotheca gracilipes* use calcium ion concentrations to identify suitable microhabitat on the underside of specific plant leaves (Wallace and Edmondson 1986). The marine bivalve *Mercenaria mercenaria* and the polychaete lugworm *Arenicola cristata* both reject disturbed sediments with lowered oxygen concentrations during recruitment (Marinelli and Woodin 2002), and juveniles of *A. cristata* also reject or accept sediments for burrowing based on ammonium levels, which appear predictive of disturbed or undisturbed conditions, respectively (Woodin et al. 1998). Qian (1999) provides a review of polychaete settlement.

In addition to producing specific chemical compounds that cue settlement, compounds from biofilms may also serve as general indicators of habitat quality for recruiting larvae. Variance in microbial presence/absence and species composition of the community is likely predictive of water quality, nutrient levels, disturbance regime, environmental toxins, and other features of the habitat. It seems reasonable that both marine and freshwater larvae would be selected to sense and act on such cues. As possible examples, larvae of the tubeworm *Hydroides elegans* settled on multiple diverse biofilms, but settlement was most strongly correlated with bacterial density rather than community composition—possibly an indicator of biofilm age and therefore habitat stability (Lema et al. 2019). Larvae of polychaete worms also sometimes recruit in response to density of certain sediment-associated bacteria (Sebesvari et al. 2013). However, not all biofilms are attractive to larvae. Specific marine bacteria associated with the alga *Ulva australis* may also inhibit settlement of fouling organisms including fungi, other bacteria, algae, and bryozoans on the surface of *U. australis* (Rao et al. 2007). Hadfield (2011) provides an extensive review of larval settlement in response to bacterial biofilms.

Anthropogenic effects on larval chemical ecology and dispersal

Anthropogenic impacts affect marine and freshwater systems not only via overfishing, pollution, acidification, warming, etc., but also by disrupting critical chemically mediated interactions upon which marine populations and communities depend. Several of these interactions are referenced above but will be re-emphasized here due to the worrisome, but largely unrecognized, potential for human activities to interfere with the critical chemical communication network that may commonly aid ecosystem function and resilience. When humans overfish reefs and advantage macroalgae over corals (Mumby and Steneck 2008), the degraded, macroalgal dominated reefs may fail to recover because both the reef fish and coral larvae that need to colonize to enhance reef resilience avoid recruiting to these areas based on a lack of positive chemical cues from corals and an overabundance of negative cues from macroalgae (Lecchini et al. 2013; Dixson et al. 2014; Brooker et al. 2016). Paralleling this, auditory cues missing from degraded reefs also reduce settlement by reef fishes in a manner that seems similar to the absence of stimulatory chemical cues (Gordon et al. 2018). Humans also are destroying native terrestrial vegetation that attracts larvae of coastal reef fishes and enhancing the abundance of non-native coastal vegetation that may repel reef fishes (Dixson et al. 2008, 2011). Even without altering the species composition of coastal vegetation, human presence alone can make chemical cues from coastal vegetation less attractive (Brooker et al. 2020).

In both marine and freshwater environments, sedimentation and chemical run-off from adjacent terrestrial regions can disrupt the ability of marine species to detect and respond appropriately to chemical cues used in reproduction, habitat selection, and settlement. Prolonged exposure to sediment deposition altered reef fish behavior from selecting live to selecting dead coral as a preferred settlement site (O'Connor et al. 2016). The ability of larval reef fishes and shrimps to respond to chemical cues of conspecifics also was significantly reduced, or even reversed, by acidified water, sediment, and pesticides (Fig. 3 compound 17) (Lecchini et al. 2017). Increased turbidity, such as that caused by sediment run-off due to coastal development, also impaired the ability of newly settled *Chromis atripectoralis* damselfish to avoid a common predator across most levels of turbidity (Wenger et al. 2013). Under elevated nutrient conditions, more barnacles and oysters settled on temperate mangrove trunks, but they also experienced heightened post-settlement mortality (Minchinton and McKenzie 2008). Certain mosquito pesticides (Fig. 3 compounds 18 and 19) stimulate larval queen conch (*Strombus gigas*) to metamorphose more readily in response to a natural algal metamorphic cue, potentially undermining their ability to discriminate habitat quality prior to metamorphosis (Delgado et al. 2013).

Ocean acidification also impacts the behavior and sensory abilities of larvae during dispersal, settlement, and early juvenile stages. Larval clownfish reared in future-CO_2 conditions of reduced pH either did not

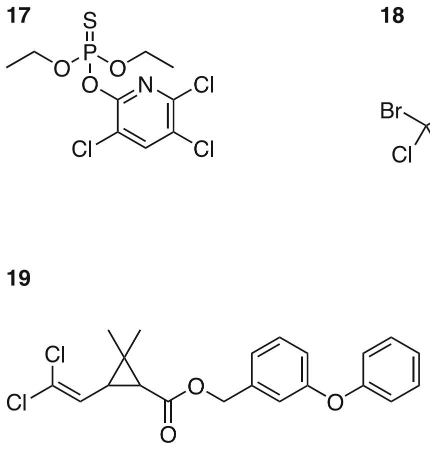


Fig. 3 Structures of pesticides that alter larval behavior. Chlorpyrifos (compound 17) is a common pesticide that impairs preference for conspecific cues in larval reef fish. Naled (compound 18) and permethrin (compound 19) are insecticides that increase queen conch larvae's responsiveness to a natural metamorphic cue

respond to, or were attracted toward, olfactory cues of predators that they would normally avoid (Munday et al. 2009), suggesting that ocean acidification may reduce the ability of some fishes to respond appropriately to cues indicative of dangers within settlement sites. Many similar studies support the conclusion that ocean acidification affects the perception of chemical cues, and associated behavior, of multiple species of larval fishes and some adults, as well as impacting other sensory systems including lateralization, vision, and hearing (summarized by Munday et al. 2020). However, a recent study using differing methodologies, and often different species, suggests that behavioral alterations such as those described by Munday et al. (2009) may not be robust across species and methodologies (Clark et al. 2020). Different species and individual fishes are known to have different sensitivities and responses to elevated CO_2 (Munday et al. 2020).

When larvae of the sea bass *Lates calcarifer* were raised under elevated CO_2 conditions, they became attracted to estuarine water, while larvae raised in present-day conditions did not exhibit this behavior (Pistevos et al. 2017). Estuaries are a post-settlement habitat for this fish, but larvae are not yet prepared for that environment and should not be attracted to it at this life stage (Pistevos et al. 2017). Non-responsiveness to cues associated with habitat for later life stages may prevent pelagic larvae from entering too early into areas with high predation (Leis and McCormick 2002) or other threats for which they are unprepared; early attraction to these cues brought on by ocean acidification would be maladaptive and interfere with larval habitat selection. Leis (2018) suggests that if predicted impacts of ocean acidification on larval and juvenile sensory systems of fishes are true under natural field conditions, fishes of the future may become subject to the passive dispersal due to physical processes that was previously assumed as a paradigm and only recently abandoned following the recognition of how important larval behavior could be in directing recruits to specific sites. Acidification may also alter the chemistry and/or microbiome of host organisms like seaweeds (e.g., Aires et al. 2018), reducing the ability of associated species to locate these hosts or food sources during settlement.

Anthropogenic introductions of novel species also may be disrupting the effectiveness of chemically cued interactions such as avoidance of consumers. There is some indication that adults and larvae in freshwater and saltwater systems may be worse at detecting the threat of invasive predators compared to native predators (Nunes et al. 2013; Benkwitt 2017; Segev et al. 2017), as has been seen in some terrestrial systems (e.g., Heiling and Herberstein 2004). Adult mosquitoes appear less effective at avoiding invasive fish predators relative to native fish predators during oviposition (Segev et al. 2017). Additionally, some native species appear to detect invasive predators via chemical cues; others do not. In the Caribbean, certain larval reef fishes avoid sites with native predators but not invasive lionfish, although this is species-specific (Benkwitt 2017).

Conclusion

Differences in physical, biological, and life-history traits of marine and freshwater systems have selected for juvenile stages that chemically assess and respond to appropriate settlement cues in marine systems but for adults to sense and respond to chemical cues in freshwater systems before depositing juveniles in appropriate habitats. In marine systems, larvae may respond to sound, hydrodynamic, or other cues across large spatial scales, but at smaller scales, where the final decisions to settle and metamorphose must be made, the critical cues are commonly chemical. Given the overwhelming fitness consequences of settlement site selection by sessile benthic species in marine systems, it seems likely that the incompletely developed juvenile stages making these decisions may rely on a “combination lock-type” sequence of cues to prevent errors in this decision making. A larva may need to receive hydrodynamic cues of being near shore, then a chemical cue of an appropriate general environment that activates a swim-down and explore behavior, and finally a contact chemical cue (or series of them) that the appropriate microsite for attachment has been found. Fewer details are known or suspected regarding the potentially complex habitat selection process for freshwater organisms, either as adults or as larvae.

In both marine and freshwater environments, juveniles (or ovipositing adults for freshwater systems) may respond positively to chemical cues from desirable habitats, prey or hosts or conspecifics, and to substrates predictive of juvenile survivorship. In contrast, negative responses are triggered by chemical cues of predators, competitors, parasites, or degraded habitats. These positive and negative responses to chemical cues and signals are not generated by within-habitat chemicals alone. Chemical cues from terrestrial vegetation, from human activities on the shore, etc., can also affect critical chemically mediated behaviors in marine and freshwater systems, making it mandatory that conservation and management efforts transcend marine, terrestrial, and freshwater boundaries.

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Declarations

Conflict of interest The authors declare no conflict of interest.

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