

Review

Do human activities influence survival and orientation abilities of larval fishes in the ocean?

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Running title: Human impact on larval fish orientation

Abstract

The larval stages of most marine fishes spend days to weeks in the pelagic environment, where they must find food and avoid predators in order to survive. Some fish only spend part of their life history in the pelagic environment before returning to their adult habitat, for example, a coral reef. The sensory systems of larval fish develop rapidly during the first few days of their lives, and here we concentrate on the various sensory cues the fish have available to them for survival in the pelagic environment. We focus on the larvae of reef fishes because most is known about them. We also review the major threats caused by human activities that have been identified to have world-wide impact and evaluate how these threats may impact larval-fish survival and orientation abilities. Many human activities negatively affect larval-fish sensory systems or the cues the fish need to detect. Ultimately, this could lead to decreased numbers of larvae surviving to settlement, and, therefore, to decreased abundance of adult fishes. Although we focus on species wherein the larvae and adults occupy different habitats (pelagic and demersal, respectively), it is important to acknowledge that the potential anthropogenic effects we identify may also apply to larvae of species like tuna and herring, where both larvae and adults are pelagic.

Keywords: climate change, larval fish, pollution, sensory systems, teleost fish

INTRODUCTION

Larval life history

Tropical teleost, or bony, reef fishes have a complex life history (Leis 1991). Most fish species on any given reef spawn pelagic eggs that are fertilized externally, after which there is no further parental involvement. The pelagic eggs drift away from the reef into the pelagic environment and hatch in a short time, usually 24 hours or less. A minority of reef-fish species have other spawning modes, including a few that are viviparous, some that brood their eggs orally, and others that deposit their eggs on a substratum and protect them until hatching (Leis 1991). In nearly all of these species, the newly-hatched young also leave the reef habitat and enter the pelagic environment. These reef-fish propagules are pelagic animals for several days to months, depending on species (e.g., Mora *et al.* 2012). They must survive, grow and develop without parental assistance during their pelagic sojourn, and at the end of this period, they need to find suitable habitats upon which to settle. Depending on species, settlement habitat may be the same as that of the adult, or it may be an intermediate nursery habitat. In either case, a pelagic animal must quickly adapt to a demersal habitat it has not previously experienced and without any direct parental assistance. Newly hatched reef-fish propagules enter the pelagic environment at a length of a few mm to a cm, and they settle at sizes ranging from less than a cm (e.g., gobies) to 20 cm (e.g., porcupinefish; Leis & Carson-Ewart 2004). Thus, the early-life history of reef fish species is all about change: major ontogenetic changes take place in size, morphology (Fig. 1), and behavior, and this is combined with major changes in habitat, prey, and predators.

During their pelagic phase, the early-life history stages of reef fishes are subject to dispersal by currents (Leis *et al.* 2011b). Determination of the spatial scale over which eggs and larvae are dispersed is important for understanding the genetic and demographic

connectivity between reef fish populations, which are subdivided by the patchy distribution of reefs and the tendency of many reef fish species to remain site-attached during their adult stages. Proper management of fisheries and marine protected areas requires an understanding of the spatial scale of population connectivity, which for reef fishes is determined mainly by dispersal of the larvae (Cowen 2002). Larvae are small, so it was traditionally assumed that they were effectively passive, and that their dispersal was determined almost entirely by the currents. However, larval reef fishes are remarkably capable animals, with swimming speeds similar to the currents in which they live, swimming endurance that enables them to swim for many hours without food or rest, orientation abilities that ensure they will not be swimming randomly, ability to determine and adjust vertical position in the water column, and good senses of hearing, sight, and smell (Leis 2006; Arvedlund & Kavanagh 2009; Leis *et al.* 2011a) (Fig. 1). There is also reason to expect that the larvae will be able to detect magnetic fields and use this for orientation (Formicki 2008).

One of the major paradigm changes in marine ecology over the past two decades has been driven by two discoveries: the behavioral capabilities of larval reef fishes, and the high degree of self-recruitment (i.e., larvae settling close to where they were spawned) found in many reef fish populations (Jones *et al.* 2009). Together, these discoveries have led many marine ecologists to conclude that dispersal of larval reef fishes is not a passive process driven primarily by physical processes, but rather a biophysical process wherein the behavior of the larvae plays a major role in influencing dispersal trajectories and outcomes. Numerical modelling of dispersal of larval reef fishes supports the importance of larval behavior to dispersal outcomes (Cowen *et al.* 2006; Paris *et al.* 2007; Trembl *et al.* 2013). Once we begin to regard the larvae as active animals with impressive behavioral and sensory abilities, a different perspective about larval dispersal is forced upon us. Chief among these behaviors is

the ability to orientate in the pelagic environment (Leis *et al.* 2011a). A variety of senses are used for orientation over a range of distances (Table 1). Many of these are capable of being disrupted by human activities, as will be discussed in the sections below.

Larvae of tropical fishes have frequently been assumed to be at much higher risk of starvation and mortality than are larvae of temperate species (Houde 1989; Doherty *et al.* 1985). This is because tropical waters are perceived to be more oligotrophic than temperate waters, with less food available for larvae that are assumed to have greater physiological demands due to higher ambient temperatures. However, recent research has shown that the feeding incidence of larval fishes in tropical waters is at least as high as in larvae from temperate latitudes (Llopiz 2013). Further, tropical larvae are more selective than are temperate larvae in the types of food they eat (Llopiz 2013). Thus, once again, the traditional assumptions have proved to be wrong. Feeding in larval fishes involves the use of vision, olfaction, and mechanoreception, largely over short ranges.

Predation on fish larvae is thought to be high, yet there is little quantitative information on this subject, especially for tropical species. Anecdotal information suggests that wild reef fish larvae, both before and after they become competent to settle, are highly aware of predators and the threat they pose, with vision, olfaction, and mechanoreception implicated as the senses predominantly used by the larvae to detect them. In contrast, reared larvae are much less reactive to predators and to divers trying to capture them (Olla *et al.* 1994; Leis, 2006). The distances over which these senses operate to avoid predation are relatively small (Table 1). Reefs are thought to be particularly dangerous places for fish larvae given the high density of predatory fishes and invertebrates found there, and it is frequently assumed that avoidance of these high concentrations of predators is a major evolutionary pressure resulting in fish larvae being found in open, pelagic waters, rather than

in the reef environment (Johannes 1978). The high mortality of young reef fish associated with settlement is thought to be due primarily to predation (Doherty *et al.* 2004).

The depth at which larvae choose to swim has profound effects on their growth, survival and dispersal. The pelagic environment is highly three-dimensional, and what appears at first glance to be a relatively featureless place, varies much more per unit distance vertically than horizontally in pressure, light, temperature, oxygen, current velocity, food quantity and quality, and predators. Vertical distribution of pelagic animals, including marine larvae, tends to be highly structured, but seasonal, diel, ontogenetic, and spatial changes are common. Larvae of most reef fishes are found in the mixed surface layers and within the thermocline (Cowen 2002; Irisson *et al.* 2010).

Behavior of larvae is important while they are fully pelagic animals, when they become competent to settle and are seeking out appropriate habitats upon which to settle at a mesoscale, and as they leave the pelagic environment and are making choices about settlement sites at the microscale (Leis 2006). Throughout these phases, the larvae use sensory cues in all their activities from feeding to settlement (Kingsford *et al.* 2002; Leis *et al.* 2011a), and it is these that we address here.

Human activities and global threats

Humans build developments on land and on the coast. They dredge rivers and harbours and generally alter the environment to suit their needs. The equipment needed to achieve this generally burns fossil fuels and in the process emits gases that alter the composition of our atmosphere and our oceans. We love seafood, and a large proportion of the human population depends on an industry that has developed various ways of extracting the sought-after types of seafood. Over 16% of animal proteins consumed by humans on this

planet comes from animals harvested from the sea, with average per capita consumption nearly doubling in the past forty years (Nomura 2009). All these activities on land and on the water extract and/or add substances and thereby change the composition of our environment more and more rapidly. What are the consequences of these activities for the other organisms living in this changing environment? Recently, this question has received more attention and a new field of study is emerging that focuses on the effects these changes may have on various terrestrial and aquatic organisms.

Most studies addressing the marine environment focus on localised disturbances that affect single species or communities. What had been missing is a more global approach that summarises the many different effects of human activities and evaluates their cumulative threat. An ambitious study has done just that (Halpern *et al.* 2008). These authors used 17 known human drivers of ecological change and created a global model to evaluate the level of threat each driver poses either alone or in combination with others. This was done for 14 habitat types within both offshore and near shore environments. Halpern *et al.* (2008) found that nearly all habitats are affected in some way, and nearly half of the world's marine habitats are affected by more than one driver. Climate change drivers (ocean acidification, UV, and ocean temperatures) affect the largest areas, both in coastal waters (depth < 200m) and offshore waters. While fishing (pelagic / demersal / non-habitat modifying and habitat modifying) affects much smaller areas, the threat scores are only slightly lower than those of climate change drivers. Pollution (chemical) received the lowest threat score, probably because its effects are still relatively localised.

Here, we concentrate on those global threats that are likely to impact larval fish survival and orientation ability during their pelagic phase (see Table 2 for summary). In the following section, we evaluate the effects of human impacts on the sensory abilities known to

be important during this stage in fish life history. We address the pelagic, early life-history phase between departure from the reef environment and settlement into demersal habitats some time later. Thus, we use an ecological definition of the larval phase rather than a morphological one. This phase might properly be referred to as the pre-settlement phase, but to conform with conventional usage, we have referred to it as the larval phase. Much of the published work stems from work on settlement-stage larval fish as they can be captured with light traps as they come in toward the reef for settlement at night (Fig. 2).

DISCUSSION

Effects on larval orientation and survival: Sensory systems

1) Olfaction

The olfactory sense is well developed in larval fish, with a high level of sensory competency reached prior to settlement (Arvedlund *et al.* 1999; Wright *et al.* 2005) (Fig. 1). Olfaction is critical for a number of behaviors, such as oriented swimming, predator avoidance, habitat selection, and conspecific recognition that are integral to survival during the journey from the pelagic zone to a suitable settlement habitat (Leis *et al.* 2011a; Ward & Currie 2013). Human-mediated changes in ocean chemistry can impact on these behaviors through the impairment of the olfactory systems and their function, and this has serious implications for the connectivity and persistence of fish populations. This inhibition and degradation of the olfactory sense, also known as olfactory toxicity, is of concern for larval fishes as their olfactory systems are particularly sensitive to waterborne contaminants (many of which are neurotoxic or impair neuron functionality), and because the olfactory sensory neurons (OSN) and the surrounding aquatic environment are generally separated only by mucus in a covered cavity (Tierney *et al.* 2010).

How are these implications likely to manifest themselves? Olfaction is important for habitat location and selection, potentially allowing for oriented swimming toward suitable habitats while the habitat is still well out of visual range. The preference of reef fish for the smell of plumes emerging from coral reef lagoons indicates that the sensitivity and potential navigation of larval fish using olfaction should be factored into dispersal models (Atema *et al.* 2002). Indeed, fish larvae from different reef species have shown behavioral changes in response to water bodies containing different chemical cues while being observed *in situ* (Paris *et al.* 2013). Innate olfactory preferences continue to play a role in the selection of microhabitats once a suitable area is located, allowing larval fish to be highly selective for habitats that maximize the chances of survival (Arvedlund *et al.* 1999).

Fish also rely on olfaction to assess predation risk as it allows predator detection at a greater scale depending on ocean conditions (Hartman & Abrahams 2000). For larval fishes, the ability to not only detect predators but differentiate their odour from non-predatory fish appears partly innate and partly learned (Vail & McCormick 2011). Larvae are able to detect predators based on olfactory cues at settlement, which is vital as predation pressure is high at this life stage and many predators are different from those in the pelagic environment (Leis & Carson-Ewart 1998; Almany & Webster 2006). A reduced ability to successfully detect suitable habitats and avoid predators would result in higher mortality and a deleterious effect on the recruitment success of larval fish, with uncertain flow-on effects for marine ecosystems (Dixon *et al.* 2010).

Manmade chemical pollutants, such as pesticides and industrial-use heavy metals, are almost ubiquitous in aquatic environments close to human settlements. Exposure to these chemicals has been documented to result in hyposmia, or the diminished sensitivity of the olfactory systems in fish (Moore & Waring 1996; Shin *et al.* 2001; Baldwin *et al.* 2011).

Indeed, common components of urban runoff such as copper, cadmium, and aluminium can damage the olfactory epithelium, while chemicals from pesticides can be linked to increased mucus coverage of the olfactory organs (Klaprat *et al.* 1988; Sloman 2007; Baldwin *et al.* 2011). It is likely that different contaminants will act in a cumulative manner meaning that even at low levels, and with each contaminant disrupting different elements of the chemosensory pathway, olfactory abilities of larval fish may be seriously impaired (Ward *et al.* 2008).

Increased predation rates of fish exposed to chemical contaminants in a laboratory setting have been documented, with juvenile trout experiencing significantly higher predation after only two hours of exposure to the insecticide carbaryl due to the inhibition of an enzyme controlling neurotransmitter signalling in olfactory sensory neurons (OSN) (Labenia *et al.* 2007). This effect has also been found in other fish species. In salmonids, perhaps the most famous example of homing behavior expressed among fishes, the return of migrating fish was lowered significantly due to toxicity of the OSN after exposure to diazinon, an insecticide known to contaminate surface waters in areas inhabited by this family of fishes (Scholz *et al.* 2000).

There are indications that the degrading effect on olfactory sensory systems in fish larvae due to increased levels of atmospheric CO₂ and the projected increases in ocean acidity may also have disturbing and unpredictable effects on important behaviors in larval fishes. Settlement-stage reef fish larvae exposed to water simulating predicted rises in ocean acidity due to atmospheric CO₂ not only lost the ability to discern predatory from non-predatory fish but were strongly attracted to the odour of predatory fish (Dixon *et al.* 2010). In reef fish larvae, olfactory responses to habitat cues also appear susceptible to changes in ocean pH. Anemonefish (*Amphiprion spp.*) larvae lose their ability to discriminate between habitat

olfactory cues when exposed to pH levels simulating CO₂ induced ocean acidification predicted to occur within the coming century, thereby reversing avoidance behavior to attraction behavior to some habitats (Munday *et al.* 2009b). At a pH level simulating the higher range of possible future acidity levels, the larvae lost their olfactory preferences altogether. Even if larvae did manage to return successfully to their natal habitat, a loss of olfactory function that normally allows larvae to discriminate between the odors of parental and non-parental fish, would make them more prone to inbreeding, again allowing for population level changes that could lead to the decline of many marine species (Munday *et al.* 2009b).

The effects of chemical contamination of the marine environment on the olfactory systems of fishes are well documented, and the behavioral changes associated with chemical contamination are wide ranging and, in some cases, drastic. If larval fish are less able to utilize this sensitive sensory modality effectively due to human-induced changes in water chemistry, the structure, connectivity, and persistence of fish communities around the world could be affected, with potentially devastating impacts on the ocean's ecosystems.

2) Vision

Vision is important for larval fishes for a variety of tasks, such as depth selection, detection of prey, predator avoidance, orientation and finally settlement habitat selection and visual communication with other fish (for review see Leis *et al.* 2011a). The cues involved in these tasks are varied and include contrast (prey/predator have to be brighter or darker than the background illumination to be seen) (Lythgoe 1979), possibly polarised light for orientation (Leis *et al.* 2003), color (habitat selection and communication) as well as the position of the sun for orientation (Mouritzen *et al.* 2013) and possibly also brightness (depth). Whether or not any of these cues are visible to the larvae depends on their visual

system, the ambient illumination, and the water quality (Lythgoe 1979). Any human activities that alter one or more of these factors will interfere with the ability of larvae to detect relevant visual cues.

Teleost fish have a duplex retina, containing rods (dim light vision) and cones (bright light vision, colour vision). The spectral sensitivity of adult fish is generally well matched to the spectral properties of their habitat (Lythgoe 1979). During development, the spectral sensitivities of the different cone types can be influenced by the spectral environment to which the fish are exposed. Studies on a wide variety of fish including barramundi (*Lates calcarifer* Bloch, 1790) (Ullmann *et al.* 2011), zebrafish (*Danio rerio* Hamilton, 1822) (Dixon *et al.* 2004) and beluga (*Huso huso* Linnaeus, 1758) (Banan *et al.* 2011) show that fish reared under abnormal ambient light conditions in the laboratory have long-wavelength shifted photoreceptor sensitivities. Fish raised under long wavelength illumination tend to be larger and mature faster (e.g., *Chrysiptera cyanea* Quoy & Gaimard, 1825) (Bapary *et al.* 2011) compared to those raised in short-wavelength conditions (but see Shin *et al.* 2012). It is thus possible that in conditions that restrict or alter the light environment (e.g., algal blooms, or oil slicks), the sensitivity of the visual system of developing larvae is shifted toward longer wavelengths (Fig. 3). A loss of short-wavelength sensitivity could prevent the larvae from detecting polarisation cues, which are postulated to aid orientation in the pelagic environment (Leis *et al.* 2011a) and may also influence their ability to detect prey due to the loss of perceived contrast between the prey and the short-wavelength rich background (Fig. 4). Any shift in spectral sensitivities also changes color perception and will influence colour communication and in extreme cases can lead to a loss of species (see section on eutrophication below).

Once visual signals are detected by photoreceptors in the retina, they are analysed partly in the retina itself and partly in higher order structures in the brain. A recent study on

the effects of ocean acidification on larval fish sensory abilities demonstrated that increased levels of CO₂ (~900ppm), such as predicted to occur around year 2100, alter neurotransmitter function (Nilsson *et al.* 2012). GABA-A receptors are found throughout the visual pathway as well as the brain in vertebrates, which would explain why all sensory systems looked at so far seem to be negatively affected. Visual predator recognition, for example, is impaired in juvenile damselfishes exposed to enhanced CO₂ levels, leading to an increased risk of predation (Ferrari *et al.* 2012). It is unclear at present whether fish may be able to adapt to increasing levels of CO₂ as all experiments expose the fish to more than double ambient CO₂ levels without intermediate stages.

Downwelling sunlight is heavily filtered by the atmosphere and the ozone layer (Madronich *et al.* 1998), and, as a consequence, only light with wavelengths between around 290nm (ultraviolet radiation, UVR) and 3000nm (infrared radiation) reaches the surface of the Earth. The filtering properties of the water depend on the composition and amount of particulate matter suspended in the water column (Jerlov 1976). Coastal waters are generally richer in dissolved organic material (DOM) compared to oceanic waters and thus transmit less light and longer wavelength light compared to clear oceanic waters (see Jerlov 1976 for quantification of different water types and their transmission properties). The amount as well as the type of particles in the water column can change dramatically due to either increased turbidity, such as caused by storms, dredging, and pollution, or to decreased turbidity, such as potentially caused by acidification (see paragraph on UV in section on Physiology).

As turbidity increases, the overall visibility is reduced and the distance over which prey/predators or settlement habitat can be detected is restricted (Fig. 5). While the visibility of any object will also depend on the visual system of each individual species, this effect is thought to be more pronounced for adult predators as they have to detect their prey over

larger distances. Indeed, the condition of older predators was found to be reduced in turbid conditions (Zingel & Paaver 2010), while the condition of larval fish was enhanced (Naas *et al.* 1992; Shaw *et al.* 2006; but see Salonen & Engstrom-Ost 2010). Larval fish are thought to be less affected by the increased scattering in turbid waters, probably because they are close range feeders and fewer light-scattering particles are between them and their prey (Fiksen *et al.* 2002; Utne-Palm 2002). Given the choice between clear and turbid waters, larvae of some fish species have been shown to prefer turbid waters (e.g., pike, Lehtiniemi *et al.* 2005), probably due to a decreased risk of predation, an increased opportunity to feed, and maybe also a decreased risk of UV damage.

Pollution can lead to eutrophication and also to increased turbidity. If nutrients are added to otherwise relatively nutrient poor waters, algal growth will be enhanced, which can ultimately lead to algal blooms. Algal blooms starve the water of oxygen and some are toxic and have been found to be lethal for plankton and fish (Anderson 1989; D'Silva *et al.* 2012). Algal blooms also alter the light environment, both in terms of intensity and spectral quality. Although fish seem to be able to cope with reductions in overall light intensity, changes in spectral quality of ambient light may lead to changes in visual sensitivity as described earlier. In extreme cases, the consequences of changed visual sensitivities together with changed ambient illumination and, therefore, signal transmission, species diversity can be reduced as has been shown to be the case for cichlids in Lake Victoria (Seehausen *et al.* 2008).

3) Mechanoreception: Hearing

Human activities can interfere with hearing in fish larvae in two broad ways: by sound or pollution induced damage to the hearing organ itself, or by masking biologically relevant sound. There is little research on the effects of intense sound, such as underwater explosions, pile driving, or military sonar, on the ears of fish larvae, but work on adult fishes (Popper &

Hastings 2009) indicates that many sounds commonly produced by humans will seriously affect hearing ability at least temporarily and may seriously damage the ear or swim bladder of larvae (the swim bladder, which is filled with gas, is probably involved with hearing in fishes (Leis *et al.* 2011a). But, as in other vertebrates, the ear of fishes is also central to balance and physical orientation, and if badly damaged, results in loss of balance. Recent research shows that the otoliths of larvae of a marine fish exposed to 2,100 μatm partial pressure of carbon dioxide (pCO_2) had increased otolith size, density, and mass (Bignami *et al.* 2013). Theoretically, this should increase hearing sensitivity, which may have impacts both positive (e.g., increased hearing range), and negative (e.g., increased background noise interference, changes in the larva's centre of gravity, its overall density or its swimming ability). However, the seemingly positive effects of increased otolith size are likely to be cancelled by the adverse effects of lower pH on hearing ability (Simpson *et al.* 2011).

Human activities in and on the sea generate a range of underwater sounds (Clark *et al.* 2009; Malakoff 2010), and these have the potential to raise background noise levels to the extent that 'natural' sounds are masked. For marine fish larvae, relevant natural sounds are frequencies less than about 2000 Hz, corresponding to the hearing range of the larvae as determined in laboratory tests (Wright *et al.* 2005, 2008, 2010, 2011). This encompasses the underwater soundscape: that is, a range of sounds that may be habitat-specific (e.g., waves breaking on shore or shallow reefs, adult fishes communicating with conspecifics or feeding on hard prey, and various invertebrates including snapping shrimps and sea urchins). Larvae of reef fishes can hear these underwater sounds and can use them to localize the source (Tolimieri *et al.* 2000, 2002, 2004; Montgomery *et al.* 2001, 2006; Leis *et al.* 2002, 2003; Leis & Lockett 2005; Simpson *et al.* 2005, 2008), which is frequently located in suitable habitats for settlement (Radford *et al.* 2010, 2011). If fish larvae do use these sounds to find

suitable habitat for settlement, then masking of them will lead to a decrease in the distance at which larvae can detect the sounds, and, therefore, a decrease in settlement to the target habitat (Simpson *et al.* 2005, 2008). Ultimately, this is likely to lead to a decrease in the abundance of adult fishes.

4) Mechanoreception: Lateral line

The lateral line is unique to fishes and to larval and aquatic adult amphibians (Webb *et al.* 2008). Both the lateral line and the ear rely on hair cells to detect motion. In the case of the lateral line it is unidirectional or oscillatory water flow, and in the case of the ear, it is sound-wave-induced motion of the otolith relative to the fish's body. The lateral line is effective in detecting motion in the near-field: that is, over a distance equivalent to a few body lengths. At or soon after hatching, larval marine fishes develop single, superficial hair cells on the epidermis. These can detect the motion of potential predators (McHenry *et al.* 2009; Stewart *et al.* 2013) or of potential prey (Jones & Janssen 1992). Somewhat later in development, the lateral line begins to form, which improves the ability of the larva to detect and locate the direction of the source of movement. In addition, with a functional lateral line, larvae are better able to initiate schooling, as the lateral line is intimately involved with schooling behavior (Partridge & Pitcher 1980). Initially, the lateral line is simply a row of superficial hair cells, but soon, a canal with the hair cells in the bottom develops along the side of the body, extending with branches and interstices over the head. The canal is later roofed over by scales on the trunk and tail, and by bone or scales on the head (Webb & Shirey 2003; Webb 2005).

Lateral-line function is most likely to be disrupted by the decrease in pH caused by increased atmospheric concentrations of CO₂ (Nilsson *et al.* 2012). However, some chemicals such as cobalt (Janssen 2000) and antibiotics such as streptomycin can inactivate

lateral line and superficial hair cells. Therefore, certain types of chemical pollution damage the lateral line, and when this takes place, one can expect decreased ability of the larvae to feed, to avoid predators, and to school. This will lead to a net increase in mortality.

5) Depth detection and vertical distribution

Larval fishes exist in a highly three dimensional environment, and selection of the appropriate depth to occupy is challenging, but important for predator avoidance, for finding food, for appropriate temperature conditions. In many cases it is also important for indirect control of dispersal, especially in selective tidal stream transport to enter or leave estuary systems (Forward & Tankersley 2001), which can be important intermediate nursery habitats for some reef fish species. It is thought that larvae accomplish this by detection of pressure, most likely via changes in pressure or volume of the gas-filled swim bladder (Huebert 2008; Huebert *et al.* 2010), but light intensity also plays a role (Huebert *et al.* 2010), as does visual detection of the bottom (Leis 2004).

Little is known about the pressure-detection sense in fishes, so other than the strong possibility that it, like many other senses, will be disrupted by lowering of pH due to higher concentrations of CO₂, it is difficult to determine what human activities may have an impact. However, intense sound or pressure changes such as those associated with explosions or military sonar can damage the swim bladder itself (Govoni *et al.* 2008), and this is likely to harm the ability to detect pressure changes.

Increased turbidity can impede the ability of fish larvae to visually determine the depth they occupy, or how high above the bottom they are swimming. As a result, the larvae may end up at a depth inappropriate for optimal survival, growth or transport.

6) Magnetoreception

The ability to detect and use the Earth's magnetic field for orientation has been documented in many species that migrate over large distances, including fish (e.g., salmonids, Walker *et al.* 1988). Magnetite has been found in various body parts of a range of fish (e.g., eels and tuna)(Moore & Riley 2009; Walker *et al.* 1984) and is thought to be involved in magnetic field detection (Walker 2008). Behavioral observations show that some larval fishes align along magnetic field lines of a static magnetic field (e.g., brown trout and zebrafish)(Formicki *et al.* 2004; Takebe *et al.* 2012). Geomagnetic imprinting as a mechanism for natal homing has just been demonstrated for the first time in adult Pacific salmon, which detect their natal streams via olfaction but navigate to the river-mouth, after more than a year in the pelagic environment, using a magnetic compass (Putman *et al.* 2013). Although we currently do not know whether larval reef fish also use a magnetic compass for orientation in the pelagic phase, it could explain how some of them (e.g., clownfish, butterflyfish) are able to find their way back to their natal reefs despite several days to weeks in the pelagic environment (Jones *et al.* 2005). Even if the larvae are not imprinted on a specific reef, having a magnetic compass would enable them to hold a bearing (for example, a larva in the Coral Sea need only swim to the west to encounter the Great Barrier Reef), or to compensate for passive displacement due to water movement.

Human activities include the deployment of electric cables in the ocean for a variety of reasons (e.g., telephone connection or power for wind farms, etc). These cables generate electromagnetic fields that alter the local magnetic field and thus have the potential to interfere with magnetic orientation and navigation, which is of concern as there are many endangered fish species relying on magnetic orientation and large scale navigation (Gill *et al.* 2012). Electromagnetic cables first became famous in this regard in the late 1980s when multiple shark bites led to faults in the deep water cables in the Canary Islands (Marra 1989). Since then, the number of such cables has increased, which means that navigating animals

have to frequently pass over them during their migrations. If these animals solely rely on magnetic orientation, their ability to navigate would be expected to be impaired when in the vicinity of such cables, some of which produce fields strong enough to be detected by ships' compasses (Ohman *et al.* 2007). Migrating animals that use a combination of both a sun compass and magnetic orientation such as described in the Monarch butterfly and some birds (Zapka *et al.* 2009; Zimmerman *et al.* 2009; Reppert *et al.* 2010) would potentially be able to compensate for these field anomalies, however future studies are required to test this.

Effects on larval orientation and survival: Physiology

So far, we have discussed the impacts various human activities have on sensory perception of the environment by larval fishes. Sensory system function is dependent on the physiology and the fitness of the fish. Larval fish must be able to swim relatively long distances to reach coral reefs and they must be healthy to be competitive when they have reached the densely populated reefs. We have already discussed one of the three climate change drivers identified by Halpern *et al.* (2008): ocean acidification. Here we discuss the other two: UV level and temperature increase.

The release of anthropogenic chlorofluorocarbon compounds has led to a reduction in ozone layer thickness that has resulted in higher levels of UVR reaching the surface of the Earth, and, in particular, in and around polar regions (Madronich *et al.* 1998). Long term data show that ozone levels (Randel & Wu 2007) and cloud cover (Masiri *et al.* 2008) are also decreasing in the tropics, resulting in increased levels of UVR above areas rich in coral reefs. As light passes through the water column, part of it is scattered, part absorbed and part transmitted (Jerlov 1976). UVR is attenuated faster than blue or green light but slower than red light, resulting in a light environment dominated by blue and green wavelengths with

increasing depth. For the waters above most coral reefs, biologically significant amounts of UVR penetrate the water to depths of at least 20 m (Dunne & Brown 1996; Tedetti & Sempéré 2006). With long term changes being observed in stratospheric ozone (Wild *et al.* 2005), changes in ocean pH and phytoplankton levels (Hoegh-Guldberg & Bruno 2010) and a predicted increase in water clarity through ocean acidification (Williamson & Zagarese 2003), the amount of UVR in the marine environment is likely to increase. High energy, short wavelength UVR is deleterious to biological systems in multiple ways: it damages DNA by dimerisation, it affects the structures of living cells by damaging proteins and lipids in membranes and chromatophores, and it impedes the function of vital processes such as photosynthesis and the replication of cells (Häder & Sinha 2005). The general consensus is that the negative effects of (elevated) UVR (reduced growth, malformation, and increased mortality) are more pronounced in early life stages (Bancroft *et al.* 2007), and that fish are highly sensitive in terms of mortality to changes (increases) in UVR (Llabrés *et al.* 2012; Sweet *et al.* 2012).

Fish possess various ways of dealing with UVR, including behavioral avoidance, natural sunscreens, and DNA repair. Whether these systems are able to somehow up-regulate to deal with increased UVR levels is currently not known. Larval fish receive a limited amount of natural sunscreens from their mother via the yolk-sac, which help protect the larvae from UVR until they are able to feed (natural sunscreens, or mycosporine-like amino acids have to be taken up via the food chain). It is currently unknown how much protection these sunscreens provide and whether fish are able to up-regulate their sunscreens in response to elevated UV levels. The only way larval fish could achieve higher protection would be to eat more or eat selectively, concentrating on organisms with high sunscreen content. It is unknown if fish are able to assess the sunscreen content of their food.

Reef fishes are thought to live close to their maximum temperature threshold. If the water temperature increases by as little as 2-4°C, most species experience significant reductions in aerobic scope (difference between maximum and minimum oxygen consumption). For a review of temperature effects on fish, see Munday *et al.* (2012). As a consequence, overall fitness will be reduced because less energy is available for important behaviors such as swimming (Johansen & Jones 2011), feeding, territory establishment, and eventually reproduction (Donelson *et al.* 2010). It is unclear whether larvae will be able to sustain the swimming speeds over the distances required to find their way back to the reef in warmer waters. No acclimatization effect was found for adult reef fish, even after exposure to elevated temperatures over several days/weeks (Nilsson *et al.* 2010), however it appears that within two generations, offspring of parents exposed to higher temperatures are able to acclimate, and their metabolic rates and aerobic scope return to normal values (Donelson *et al.* 2012).

Summary and conclusions

We have analysed the known or suspected consequences of human activities sense by sense and found a multitude of mostly negative consequences of human activities for larval fish survival as well as orientation ability. We are only starting to understand some of the amazing sensory abilities larval fish possess, and there is still much to be discovered about how these tiny fish use their sensory systems to not only survive the pelagic phase but also find their way back to a reef to settle. Based on the multitude of human impacts on almost every feature of the marine world, it seems unlikely that we will get the chance to understand how larval fish use various environmental cues to achieve this.

It is important to remember that fish will use a combination of cues and senses, and that all behavioral reactions initiated as the consequence of the detection of a cue will be

affected by changes in the physiology of the fish. Most studies available on the effects of human activities on reef fish address a single sense and a single threat, although the combination of elevated CO₂ and temperature has received some attention (Munday *et al.* 2009a). One might think that if one sense is impaired other senses will become more important; however, in some cases the input of two senses is required to elicit a response, as is the case for the fountain darter (*Etheostoma fonticola* Jordan & Gilbert, 1886)(Becker & Gabor 2012). A combination of chemical and visual cues is required to initiate an anti-predator response in this species. In addition, no anti-predator response was observed in conditions of elevated turbidity. Although it is useful to control as many parameters as possible in experimental studies, this study demonstrates the need for a more comprehensive approach to increase our understanding of the complex interactions of stressors as well as their combined effects on the ability of fishes to survive and successfully reproduce.

Overall, although the focus of many labs has shifted to investigating climate change effects on marine organisms, there is still limited information available, in particular for animals that are hard to access, such as larval reef fishes and pelagic fishes in general. Based on the information we have so far, we can conclude that larval fishes will be affected – mostly negatively - in some way by the various stressors human activities have created. Just what the exact consequences will be for larval fish survival, population connectivity, and overall fitness requires further analysis, but there is ample cause for concern, and targeted research is necessary to address this complex issue.

ACKNOWLEDGMENTS

We would like to thank Prof. Jiakun Song for inviting our participation in the symposium and for supporting UES' travel to and around Shanghai, Prof. Jiakun Song, Prof. Art Popper, and Prof. Shaun Collin for co-organising the meeting in Shanghai and stimulating the discussions on human impacts on marine organisms. This work was supported by an ARC Discovery grant (DP 110100695) to UES and JML.

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Table 1 Sensory organs and modes used by larvae of demersal reef fishes for various functions. ‘Yes’ indicates published evidence; ‘No’ indicates no published evidence; ‘Possibly’ indicates theoretical evaluation or equivocal indications. (i) indicates the possibility of imprinting of embryos or newly hatched larvae. Spatial scale over which the sense operates for each function is given.

Function	Eyes: Vision	Lateral line: Mechano - reception	Ears: Hearing	Nose: Chemo- reception	Magnetic sense: Magneto- reception	Swim bladder: Baro- detection	Portion of pelagic phase
Feeding	Yes: few mm to few m	Yes: a few body lengths	No	Yes: mm to a few m	No	No	Throughout
Predator avoidance	Yes: mm to 10 m	Yes: a few body lengths	Possibly: scale ?	Yes: mm to several m	No	No	Throughout
Vertical distribu- tion	Yes: to 100s m	No	No	No	No	Yes: mm to kms	Throughout
Pelagic orientation	Yes: up to 30 m plus many km	No?	Yes: up to many kms	Probably: up to many kms	Possibly: up to many kms	No	Most
Locating settlement habitat at a meso scale	Yes: up to 30 m plus many km	No	Yes (i): up to many km	Possibly (i): up to 10s of kms	No	Yes: up to several 100 m	Near end
Locating settlement habitat at a micro scale	Yes: up to 30 m	No	Possibly (i): up to several 10s m	Yes (i): up to several 10s of m	No	Yes: up to several 10s of m	At end

Table 2 Human stressors (Halpern *et al.* 2008) and impacts on sensory systems used by larvae of demersal reef fishes. ‘Yes’ indicates published evidence; ‘no’ indicates no published evidence; ‘possibly’ indicates theoretical evaluation or equivocal indications.

	Climate Change			Pollution		Fishing	Dredging
SENSE	temperature	acidification	UV	organic and inorganic	sound, electro-magnetic	demersal, habitat modifying	turbidity
Vision	possibly	yes	yes	yes	no	possibly	yes
Mechano-reception	possibly	possibly	no	possibly	yes, low frequency	no	no
Hearing	possibly	yes	no	possibly	yes	no	no
Chemo-reception	possibly	yes	no	yes	no	no	no
Magneto-reception	possibly	possibly	no	possibly	yes	no	no
Baro-reception	possibly	possibly	no	no	no	no	no
Physiology	yes	yes	yes	yes	no	no	no

Figure 1 Larval development of a common coral-reef fish, the pomacentrid, *Pomacentrus amboinensis*. This species hatches from demersal eggs guarded by the adult male. Age is in days after hatch (DAH); sizes given are standard length. Details and illustrations from Murphy *et al.*, 2007 unless noted otherwise. Data on mean swimming speed and endurance from Fisher *et al.*, 2000.

(a) 2.5 mm, 0 DAH, yolk-sac preflexion-stage. Note incompletely pigmented eye and apparently non-functional mouth. Superficial sensory hair cells are scattered over the body, and a small, round patch of olfactory cilia is present on the snout. The yolk occupies most of the gut region. A median fin fold and paired pectoral fins are present. Day one larvae have a critical speed of 3.5 cm s^{-1} , and endurance of 0.5 km.

(b) 2.8 mm, 1 DAH, preflexion-stage. Mouth is now open and eyes pigmented and presumably functional. A shallow pit on the snout contains a few olfactory cilia, and the retina consists of cone cells. No separate yolk is visible. Day 3 larvae have a critical speed of 2.5 cm s^{-1} .

(c) 3.7 mm, 6 DAH, preflexion-stage. Critical speed at day 6 is 7 cm s^{-1} .

(d) 4.6 mm, 7 DAH, flexion stage. The caudal fin is forming.

(e) 6.0 mm, 11 DAH, postflexion stage. The nasal pit is in the process of being roofed over, most rays in the fins are formed, and pelvic fins are present. At day 12, critical speed is 11 cm s^{-1} .

(f) 7.3 mm, 13 DAH postflexion stage. Some scales are present, but are not illustrated. Twin nasal nares now provide access to the olfactory cells in the nasal capsule, and rod cells have appeared in the retina.

(g) 8.8 mm, 15 DAH postflexion stage. Scales are present over most of the body, and the lateral line is formed, but neither are illustrated. By 17DAH the pigment layer in the eye can move, allowing light adaptation of the retina. On day 15 critical speed is 25 cm s^{-1} , with endurance of 15 km, without food or rest.

Image credit: Drawings were done by Brigid Murphy and Jeff Leis, with inking by Suzanne Bullock.

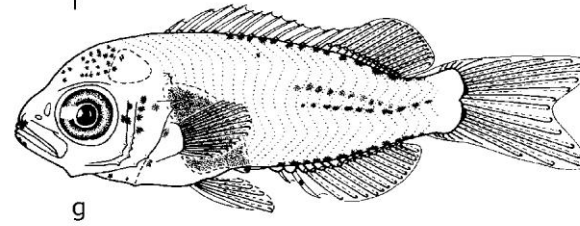
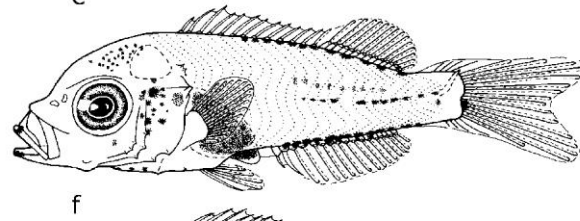
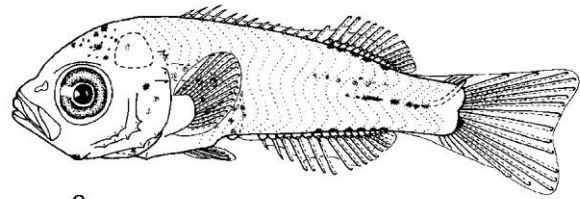
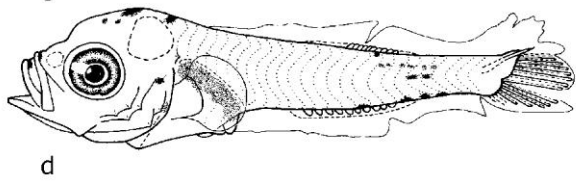
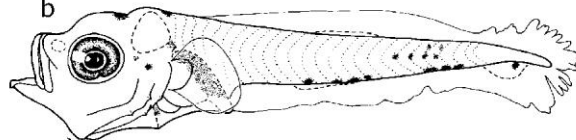
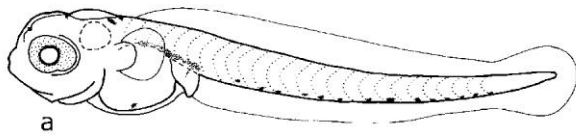


Figure 2 Examples of settlement stage larval reef fish caught in light traps at the end of their pelagic phase. This range of larval morphologies shows how developed reef fish can be before they settle and metamorphose from pelagic to demersal animals. Top left to bottom right: *Acanthurus* sp.[Acanthuridae], *Plectropomus leopardus* [Serranidae], *Pomacentrus amboinensis* [Pomacentridae], *Dischistodus* sp [Pomacentridae], *Chelmon rostratus* [Chaetodontidae], *Chaetodon plebeius* [Chaetodontidae], *Stegastes* sp. [Pomacentridae], *Neoglyphidodon nigroris* [Pomacentridae], *Zebrasoma veliferum* [Acanthuridae], *Holocentridae* sp. scale bar = 10mm. Photo credit: Ulrike Siebeck



Figure 3 Reef near Lizard Island, Great Barrier Reef, Australia, photographed (a) in the green (490nm-560nm) and (b) the UV (350-380nm) part of the spectrum. The contrast of different objects and their background depends on the light spectrum. Any shift in photoreceptor sensitivities or light spectrum (due to algal blooms or oil slicks) will have effects on how the underwater world appears to the fish. Photo credit: Tom Cronin

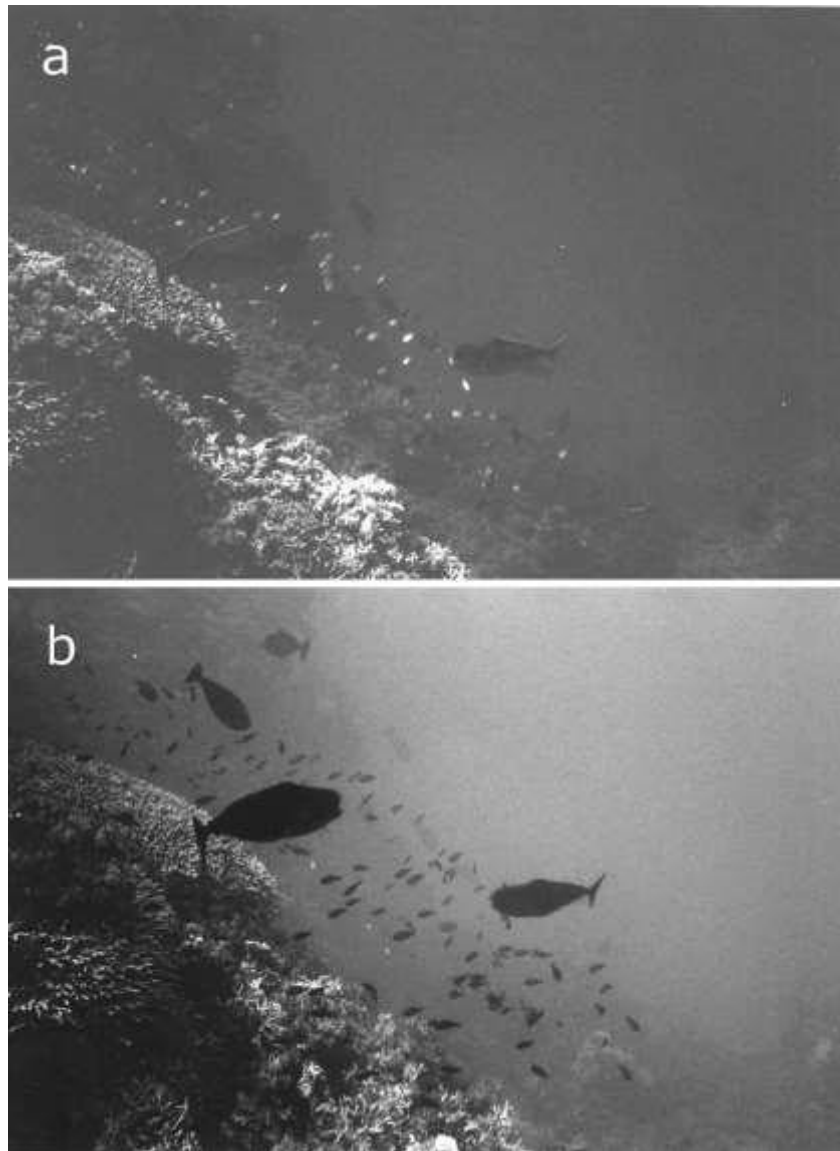


Figure 4 Plankton particles photographed with (a) and without UV present (b). UV-absorbing plankton are more visible in front of the UV-scattering background (a). Detection is much harder in conditions in which UV is reduced or absent (b). Photo credit: Ellis Loew

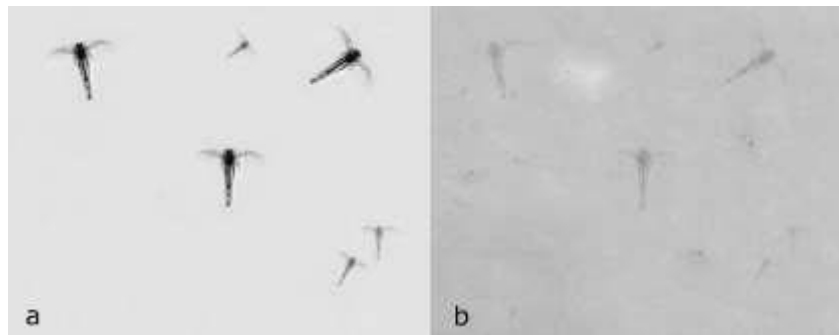


Figure 5 Example of how turbidity (increased sediment e.g. through dredging or storm activity) effects object detection. Scattering is increased and object detection (prey, predator or habitat) is impaired. Images a and b show normal conditions while images c and d show the same two locations with increased turbidity. Photo credit: Christoph Braun

