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Temporal constraints on predation risk assessment in a changing world

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HIGHLIGHTS

- We have limited understanding of how long chemical alarm cues persist after release.
- We examined the effect of UV radiation and CO_2 on persistence of fish alarm cues.
- Alarm cues of coral reef fish degrade surprisingly quickly under natural conditions.
- Anthropogenic changes have the potential to change rates of cue degradation.
- Trait-mediated indirect interactions will be altered with a changing climate.

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ABSTRACT

Habitat degradation takes various forms and likely represents the most significant threat to our global biodiversity. Recently, we have seen considerable attention paid to increasing global CO_2 emissions which lead to ocean acidification (OA). Other stressors, such as changing levels of ultraviolet radiation (UVR), also impact biodiversity but have received much less attention in the recent past. Here we examine fundamental questions about temporal aspects of risk assessment by coral reef damselfish and provide critical insights into how OA and UVR influence this assessment. Chemical cues released during a predator attack provide a rich source of information that other prey animals use to mediate their risk of predation and are the basis of the majority of trait-mediated indirect interactions in aquatic communities. However, we have surprisingly limited information about temporal aspects of risk assessment because we lack knowledge about how long chemical cues persist after they are released into the environment. Here, we showed that under ambient CO_2 conditions (~385 μatm), alarm cues of ambon damselfish (*Pomacentrus amboinensis*) did not degrade within 30 min in the absence of ultraviolet radiation (UVR), but were degraded within 15 min when the CO_2 was increased to ~905 μatm. In experiments that used filters to eliminate UVR, we found minimal degradation of alarm cues within 30 min, whereas under ambient UVR conditions, alarm cues were completely degraded within 15 min. Moreover, in the presence of both UVR and elevated CO_2, alarm cues were broken down within 5 min. Our results highlight that alarm cues degrade surprisingly quickly under natural conditions and that anthropogenic changes have the potential to dramatically change rates of cue degradation in the wild. This has considerable implications for risk assessment and consequently the importance of trait-mediated indirect interactions in coral-reef communities.

1. Introduction

On a global scale, habitat destruction is one of the “Big Five” drivers of biodiversity loss (Anthony et al., 2008; Hoekstra et al., 2005; Rohr et al., 2006; Salo et al., 2007). Loss of habitat, such as that which would occur with deforestation and mining activities, is often a rapid process with dramatic consequences that are easy to observe. In contrast, habitat degradation effects are often more subtle, slower to appear and/or harder to detect (Doak, 1995). The ubiquitous nature of habitat degradation and its more subtle effects likely means that it represents our most significant threat to biodiversity. Coral reefs are one of the most impacted and vulnerable ecosystems in the world. Indeed, nearly 30% of the world's coral reef ecosystems have already been destroyed or severely degraded (Goreau et al., 2000) and 60% of them are now facing extinction by 2030 (Carpenter et al., 2008; Wilkinson, 2002).

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Until recently, overfishing and pollution were thought to be the two major drivers of degradation in coral reef ecosystems (Hughes et al., 2003). However, climate change is an ever increasing concern. In particular, ocean acidification (OA) caused by an increase in global emissions of CO_2, sulphur oxide (SOx) and nitrogen oxide (NOx), is front and centre, and has been linked to fundamental chemical processes such as metal speciation (Miller and Frank, 2009) and fundamental biological processes, including metabolism, growth, calcification and reproduction (Fabry et al., 2008; Hassellöv et al., 2013; Kroeker et al., 2010; Widdicombe and Spicer, 2008). Whilst the vast majority of OA work has focused on calcifying organisms, damselfishes have become the model system to study OA effects on fishes (Ferrari et al., 2011a, 2011b; Munday et al., 2010). We have considerable evidence that fishes exposed to elevated CO_2 have impaired responses to risk cues as a result of cognitive impairment (Chivers et al., 2014; Nilsson et al., 2012). Fish exposed to elevated CO_2 fail to respond to risk cues and this is associated with higher mortality in the wild (Ferrari et al., 2011a).

Another threat to coral reef fish communities, particularly in the southern hemisphere, stems from stratospheric ozone depletion and its consequences for elevated ultraviolet radiation (UVR). We have seen limited work on understanding the effects of changing UVR in the past decade, likely because UVR is seen as a less pressing threat to our biodiversity. The implementation of the Montreal Protocol in 1989 is often touted by the United Nations as the single most successful international agreement, and has ameliorated much of the global ozone depletion. However, it is difficult to ascertain how consistent ozone recovery will be, due to factors such as changes in cloud cover, air pollutants and aerosols, all of which are influenced by climate change (McKenzie et al., 2011). Compared to 1980, UV-B irradiance towards the end of the 21st century is projected to be lower at mid to high latitudes by between 5 and 20% respectively, and higher by 2–3% in the low latitudes. This means that depending on where an organism lives, it has seen considerable change in UVR and could continue to see substantive changes over the next century. Changes in UVR at a local scale are dramatically influenced by turbidity and dissolved organic carbon, both of which have increased dramatically in costal marine habitats (Wenger and McCormick, 2013).

Our work here addresses fundamental questions about temporal dynamics of risk assessment in coral reef fish and provides critical insights into how both OA and UVR can influence this assessment. Prey animals have numerous sources of information available to assess their risk of predation. However, with each source of information come specific constraints. Visual cues, for example, provide information about risk in real space and time. Prey can judge the size and distance from predators and may even be able to determine the predator's motivation to feed (Murphy and Pitcher, 1997). However, the prey actually needs to be present at the correct time to acquire the information. In contrast, chemical sources of information persist for some time after they are released, and consequently provide information even after the predator has moved on from the area. However, the drawback of this information source is the temporal and spatial disconnect with the source of risk. When a prey animal detects a chemical cue that indicates risk, does it know the age of the cue? Was the cue just recently released or was it released minutes or hours or even days ago? Was the cue released in the exact location where it is being detected or was it released at a considerable distance and transported by air or water currents? There are many hundreds of studies that have investigated the role of chemical information in risk assessment, but we know surprisingly little about temporal aspects of assessment because we have only a rudimentary understanding of how long chemical information sources persist under natural conditions (Chivers et al., 2013; Ferrari et al., 2010; Wisenden and Chivers, 2006). Understanding the availability of those cues to prey species is crucial to understanding community dynamics. Chemical cues are often the basis of trait-mediated indirect interactions, which are quantitatively much more important than the direct consumptive effects of predators (Preisser et al., 2005). The detection of risk-related chemicals has been shown to mediate many inducible morphological defences, the timing of crucial ontogenetic switches, and changes in life-history strategies, affecting growth rate, age at maturation and a number of reproductive traits (Appleton and Palmer, 1988; Brönmark and Miner, 1992; Chivers et al., 2001; Hoverman et al., 2005). They also mediate the expression of antipredator behaviours, as seen in habitat and food preference and mate choice (Lima, 1998; Stankowich and Blumstein, 2005). Any factors that will affect the availability of these cues in the medium will also affect the number of individuals that will detect and respond to these cues, with dramatic implications for the existence, type, strength of many trait-mediated indirect interactions (Ferrari et al., 2010).

There are several sources of chemical information available to prey for risk assessment, including predator odours, cues from injured conspecifics or heterospecifics (alarm cues), and disturbance cues released from prey that have been disturbed by predators (Ferrari et al., 2010; Kats and Dill, 1998; Vavrek et al., 2008; Wisenden et al., 1995). From a temporal risk perspective, we know that some predator odour cues may last for upwards of several days (Fraker, 2009; Peacor, 2006), whilst alarm cues may last for hours (Wisenden et al., 2009) or may be degraded within 30 min (Chivers et al., 2013; Ferrari et al., 2007b). Chivers et al. (2013) were the first to document that the rate of degradation of alarm cues, as measured by the response of fish to the degraded cues (fish bioassay), was dependent on time of day. They showed that alarm cue breakdown in ambon damselfish (*Pomacentrus amboinensis*) occurred within 30 min in mid-afternoon, but both early and late in the day, the cues remained active for greater than this length of time. Peak breakdown of cues early in the afternoon suggests that UVR, or other abiotic factors (temperature, dissolved oxygen, pH, etc.) that fluctuate on a daily basis, may facilitate the degradation process. Moreover, microbial activity in the water column and in the sand may peak in early afternoon leading to faster degradation.

Here, we provide the first empirical test of factors responsible for variation in the rate of breakdown of chemical alarm cues and address how anthropogenic change influences rates of breakdown. This information will allow us to understand temporal dynamics of risk assessment, and even more critically how this assessment may be changing in impacted ecosystems. We examined the role of CO_2 in influencing the rate of breakdown of alarm cues, by supplementing our water with CO_2 at levels predicted to occur near the end of the century. We also test whether levels of UVR influence the rate of degradation by allowing alarm cues to degrade under natural conditions or under conditions of reduced UVR.

2. Methods

2.1. Fish collection, study species and maintenance

All experiments took place in October and November 2013, at the Lizard Island Research Station, Great Barrier Reef Australia (14°40′S, 145°28′E). We used light traps set at night to capture larval *P. amboinensis,* measuring approximately 12–14 mm total length (Meekan et al., 2001). Fish were captured approximately 100 m off the fringing reef at the end of their pelagic phase just prior to settlement to the reef. Fish were taken to the laboratory, held in 25-l flow-through tanks for a minimum of 4 days prior to the start of the experiment and were fed ad libitum with newly hatched brine shrimp three times per day. The fish grew to approximately 13–16 mm in total length prior to being used as test animals and alarm cue donors in our experiments.

P. amboinensis is a common member of the reef community in the Indo-Pacific and inhabits the edge of the reef amongst patches of sand, live and dead coral. Juveniles sustain high mortality immediately after settlement in large part due to their inability to recognize predators (Hoey and McCormick, 2004; Mitchell et al., 2011). Learning the identity of local predators is facilitated through the coincidence exposure of the fish to chemical alarm cues and unknown predator odours. Such learning