

UNIVERSITY OF GRONINGEN

MSC ECOLOGY & CONSERVATION ESSAY

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**A deep dive into seascapes of fear: how perceived predation risk alters spatial distribution of aquatic animals and its consequences.**

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## Abstract

Predation is a strong selective force in nature, and prey thus require an adaptive behavioral response. One way by which prey may defend themselves from predation is through movement, both on large scale (such as migrations) and small scale (such as within habitat use). The resulting non-random distribution of individuals, populations and communities may have ecological consequences. These consequences are not well-understood, especially for aquatic systems. In aquatic systems, anti-predator responses are varied, and dependent on a variety of factors. I found that aquatic organisms may alter their migratory timing, routes and propensity when under risk of predation. However, some other species did not show such a response, possibly due to a lack of reliable predation risk. On a smaller scale, organisms responded by moving within and between habitats on various scales. These movements may be dependent on alarm cues, predator species and individual differences. The ecological consequences of these movements may be vast, but research remains surprisingly limited. Perhaps we could increase our understanding of aquatic anti-predator behavior and its consequences by comparing aquatic and terrestrial systems.

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## Introduction

Predation is a major selective agent in the natural world, as a single unfortunate encounter of an individual with a predator can result in injury or even death. This requires adaptive behavioral adjustments from prey, such as increased vigilance or seeking out refuges when predation risk is high (e.g. Trussell et al. 2006). While such anti-predator behaviors may help in avoiding capture, they come at the cost of other activities such as foraging or mating opportunities, and are thus quite costly. Prey thus face a trade-off between risk of being predated and benefiting from engaging in other beneficial activities, such as foraging and reproducing (e.g. Wirsing et al. 2008). For example, bolder individuals may have more access to resources, but also have a higher chance of being predated (Hulthén et al. 2017). Both predation risk and anti-predator defense trade-offs differ spatially (some habitats may provide more, but riskier foraging opportunities), or temporally (foraging at night may be safer, but yields less resources) (Mittelbach et al. 2014), which can explain the observed variation of anti-predator behavior between individuals, populations and species (Bolnick et al. 2011, Mittelbach et al. 2014).

One of the ways through which organisms may avoid predation is through adjusting their movement and distribution between or within habitats. Most animals are mobile during some parts of their lives, and move around to find mates, acquire food, and to avoid predators (Nilsson et al. 2014). Some habitats and terrains are more dangerous than others, and prey will thus perceive their predation risk differently across different environments (Laundre et al. 2010). Assuming that individuals can learn to differentiate between risky and safe environments before they are killed, they will adjust their habitat use and movement accordingly, a concept known as the landscape of fear (Laundre et al. 2010). These changes in movement and habitat use can happen at multiple spatial scales, ranging from long range migration and dispersal (Hulthén et al. 2015) to small-scale movements within the same habitat (Wirsing and Ripple 2011). The result of these movements is a non-random distribution of individuals, populations and species on various scales, which can have far-reaching consequences. Examples include altered meta-population dynamics on population level (Nilsson et al. 2014), altered community composition and species interactions on the community level (Wolf and Weissing 2012), and changes in abiotic conditions on the ecosystem level (Brönmark et al. 2014). Predators can thus have quite significant non-lethal effects on communities and even ecosystems, which rival with or even completely overshadow direct effects of predation (Trussell et al. 2006).

Perhaps the most famous example of non-lethal effects in a landscape of fear can be found in Yellowstone National Park, where wolves (*Canis lupus*) were reintroduced into the area after an absence of fifty years. The large herbivores that were already present in the environment gradually altered their behavior, becoming more vigilant over time (Laundré et al. 2001). The herbivores also shifted their foraging to different habitats in response to wolf predation, at the cost of diet quality of the herbivores (Laundre et al. 2010). This change in landscape use by herbivores changed vegetation species composition, nitrogen mineralization in grasslands, and changed the predator community, all with their own respective cascading effects (Laundre et al. 2010).

Despite this well-known example, the indirect effects predators can have in landscapes of fear in general are not very well understood, especially in aquatic ecosystems. Since the non-random spatial distribution of organisms can have a wide range of ecological implications, I will investigate how aquatic organisms change their spatial distribution in response to perceived predation risk, and the resulting consequences. To start, I will quickly summarize the variety of anti-predator behaviors in aquatic organisms. Then I will review spatial anti-predator responses on large (migratory behavior) and

small (within and between habitat distribution) scales, and their ecological consequences. I will end with a discussion on the shortcomings of this essay and suggestions for future research.

## Variation in anti-predator behavior in aquatic environments

Anti-predator behaviors of aquatic species are very diverse, spanning many spatial and temporal scales, ranging from shortly increasing vigilance to changes in migratory patterns. Moreover, anti-predator responses are seen for a variety of species, ranging from large marine mammals (Wirsing et al. 2008) and turtles (Heithaus et al. 2007 p. 20) to fish (e.g. Hartman and Abrahams 2000) and water insects (Åbjörnsson et al. 1997). Anti-predator behaviors may differ between different species (Ford and Reeves 2008) or even between individuals (Hulthén et al. 2017) under different environmental conditions (Martin et al. 2010)

Abiotic conditions appear to play an important role in determining the anti-predator response. For example, individuals may change their anti-predator response under varying levels of turbidity (Leahy et al. 2011). Organisms in aquatic environments primarily rely on their visual and chemical cues to detect predators. Therefore, it was hypothesized that under low visibility conditions, organisms will rely more on chemical cues instead of visual cues to compensate for the loss of visual information (Leahy et al. 2011). Experimental evidence reveals that this is indeed the case. Spiny damselfish (*Acanthochromis polyacanthus*) were exposed to chemical alarm cues under no, low and high turbidity conditions. The fish showed significantly reduced (feeding) activity compared, and showed a similar (though non-significant) trend for area use compared to the clear water control, both of which are anti-predator behaviors (Leahy et al. 2011). Other abiotic factors, such as CO<sub>2</sub>-concentrations (Munday et al. 2016), salt concentrations (Hintz and Relyea 2017), and acoustic disturbance (Spiga et al. 2017) may also alter anti-predator responses.

Besides abiotic conditions, life history may also play an important role in shaping anti-predator behavior. For instance, some organisms may change their reaction to alarm cues as they age. Young and small pumpkinseeds (*Lepomis gibbosus*) feed mostly on invertebrates, and show an anti-predator response when exposed to chemical alarm cues. As pumpkinseeds mature, they switch to a piscivorous diet, after which chemical alarm cues now elicit a foraging response (Golub et al. 2005). Sex can also play an important role. Bahamas mosquitofish (*Gambusia hubbsi*) female fecundity is directly related to weight, which could give females a high motivation to forage, while also making them more sought-after prey. Females thus face a strong trade-off between higher weight and reproductive success, and higher chance of predation, which could lead to a more severe response to predation risk. Feeding behavior of wild-caught males and females from both low-predation and high-predation environments was recorded under laboratory conditions. It was revealed that females foraged more than males, and that females from the low-predator regime foraged and consumed significantly more than those from the high-predator regime, demonstrating that differences in predation risk can lead to behavioral changes, and that these changes can differ strongly between sexes (Pärssinen et al. 2021). While all of the examples above are by no means exhaustive, they do illustrate that anti-predator defenses are widespread, and dependent on a wide variety of factors. In the next section I will discuss how perceived predation risk can affect migratory behaviors, and its possible ecological consequences.

## Large scale movements

### Predation-induced altered migratory movements

Migrations, where animals pursue improved safety, foraging conditions, and mating opportunities (often in predictable patterns), are ubiquitous in the natural world (Bauer and Hoye 2014). Migrations are the result of a variety of intrinsic factors (physiology, genetics, etc.) and extrinsic factors (weather, food availability, etc.) (Bowlin et al. 2010). Predation is one of these migration-shaping factors.

### Migratory propensity and timing

For example, the roach is a common seasonally migratory freshwater fish, that is known to avoid predation risk by migrating from food-rich lakes to safer streams, at the cost of foraging opportunities. Experiments have revealed that this migratory behavior is plastic, making these fish an ideal candidate for experiments on perceived predation risk on migratory behavior. Hulthén et al. (2015) investigated whether increased perceived predation risk of roach from the Swedish Lake Krankesjön prior to migration affected migratory behavior by exposing small (lower indirect predation risk) and large (higher indirect predation risk) groups of roach to either a piscivorous pike (*Esox lucius*) in a separate compartment (direct predation risk) or a control. These fish were then tagged, released back into the lake and followed during migration. A significantly higher proportion of fish migrated when exposed to the predator, while individuals with high indirect predation risk migrated significantly earlier than individuals with a low indirect predation risk. These results show that both direct and indirect predation risk can influence decision-making and migration timing for facultative migrators (Hulthén et al. 2015).

### Migratory routes

Predation may not only affect migration timing, but also migration routes. Some baleen whales (Mysticeti) undertake much more extensive migrations than roach, from high-latitude feeding grounds in winter to low-latitude calving grounds in summer. While the exact mechanisms behind these migrations remain a topic of debate, it does appear that killer whale (*Orcinus orca*) predation at least is an important shaping force in migratory behavior for baleen whales (Ford and Reeves 2008). Some whale species actively defend themselves from killer whale attacks, also known as a fight response. Other species prefer to flee from attacks, a flight response. Fighting species prefer to migrate to shallow waters, and stick close to the shoreline, as these waters provide favorable conditions for whales to defend neonates and themselves from predator attacks. Older individuals, who are less likely to get predated, swim in deeper waters and do not follow the shoreline as much as individuals who are more at risk (Ford and Reeves 2008). However, this type of predictable and confined migration may also provide reliable hunting opportunities for killer whales. There must be some other benefits for offshore migration that mitigate or outweigh the predation risk (Ford and Reeves 2008). Migratory patterns of fleeing species are not so well understood, and destinations may be very spatially diffuse. These species may not have discrete calving grounds near the shore, as they would require open waters to escape. Being in close proximity to the shore will increase the chance of capture, as it is easier to get confined or to get beached in shallow waters (Ford and Reeves 2008). Predation risk thus appears to shape migratory routes, depending on other anti-predator strategies (i.e. fighting or fleeing).

## Lack of predictable risk on migrations

However, it is argued that some highly mobile prey that migrate over large distances (tens to hundreds of thousands of square kilometers) may not show spatial anti-predator behaviors at all, due to a lack of consistent and predictable predation risk. Loggerhead turtles (*Caretta caretta*) seasonally migrate along the eastern North American coast. Tiger sharks (*Galeocerdo cuvier*) often predate loggerhead turtles, and are also present in these areas. Turtles may thus face a trade-off between predation risk and beneficial activities such as feeding and mating. Hammerschlag et al. (2015) investigated whether highly mobile loggerhead sea turtles also displayed altered behavior in response to tiger shark predation by tracking wild loggerhead turtles and tiger sharks along the eastern North American coast for multiple years. They found that the loggerhead turtles did not display increased risk avoidance behavior with increasing tiger shark territory overlap. The reasons behind this remain somewhat unclear, and hypotheses include a lack of consistent and predictable predation risk, but also effects of temperature, or that the population of both species are below ecologically functioning densities. Whatever the cause may be, apparently, predation risk does not play a decisive role in turtle distribution or behavior. In fact, it appeared that shark distribution was driven by turtle movements, instead of the other way around (Hammerschlag et al. 2015). It should be noted that the conclusions from this study are based on correlation rather than causation. However, experimental testing is unfeasible considering the nature and size of the system. All in all, it would seem that migratory (and other anti-predator) behaviors may be dependent on the species and size of the system.

## Emigrations

Instead of seasonal migrations, like the aforementioned roach or whales, some organisms may emigrate. For example, grousewinged backswimmers (*Notonecta undulata*) are water insects that emigrate from areas with a high predation risk (Baines et al. 2015). This is in line with the general theory that individuals should move away from dangerous areas to maximize their fitness. However, while predation risk may promote dispersal in some animals, it can also restrict movement in others. For instance, matured offspring of the cichlid *Neolamprologus pulcher* may face increased predation risk when dispersing, and stay more grouped as a result (Groenewoud et al. 2016). So, perceived predation risk may alter migratory behavior of aquatic organisms in a variety of ways (Table 1).

## Ecological consequences of altered large scale movements

### Significance of migration

The consequences of altered migratory behaviors on the ecosystem can be vast. Migrants transport nutrients, parasites and seeds/spores with them as they travel, and forage and get predated upon along the way. As a result, migrating animals (and thus also changes in migratory behavior due to perceived predation risk) can have profound effects on food webs, communities and ecosystems (see Bauer and Høye 2014 and Brönmark et al. 2014 for reviews on animal migrations and their consequences). For example, Norwegian spring-spawning herring (*Clupea harengus*) consume  $23 \times 10^6$  tons of the copepod *Calanus finmarchicus* during their migrations, during which they transport  $1.3 \times 10^6$  tons of biomass annually. This is the world's largest flux of energy caused by a single population (Varpe et al. 2005). Animals and humans alike are dependent on these herring migrations. Herring eggs are consumed by a variety of predators, such as haddock (*Megalogrannus aeglefinus*) and lobsters. In fact,



changes in migratory patterns of herring may have been the cause of reduced lobster landings in Norway by fishermen (Varpe et al. 2005). Herring themselves are consumed by killer whales (*Orcinus orca*) and minke whales (*Balaenoptera acutorostrata*) (Lindstrøm et al. 2002, Varpe et al. 2005). Changes in migratory patterns might thus also lead to a change in whale distribution and/or diet (Lindstrøm et al. 2002, Varpe et al. 2005). In short, many organisms depend on migrating species, and changes in migratory behavior might thus have an impact on species densities, distribution and food-web interactions.

Habitats may even be shaped by migrations. Migration of salmon (Salmonidae) from the North Pacific Ocean to their natal streams not only affects biotic, but also abiotic properties of the both aquatic and the surrounding terrestrial habitats (Holtgrieve and Schindler 2011, Bauer and Hoye 2014). In lakes and streams, salmon presence increased nitrogen and phosphorus concentrations by up to 190% and 390% respectively (Holtgrieve and Schindler 2011). However, primary producers decreased in biomass, coupled with a strong increase in ecosystem respiration and decrease in gross primary production (Holtgrieve and Schindler 2011). When salmon were present, the aquatic ecosystem as a whole switched from autotrophic to strongly heterotrophic. Salmon presence also increased air-water gas exchange tenfold, drastically altering riparian vegetation, stream insect phenology and phytoplankton community structure as a result (Bauer and Hoye 2014). Migrations may thus shape entire ecosystems.

### Changes in ecosystem structure

While herring and salmon (to my knowledge) do not alter their migratory behavior in response to perceived predation risk, these examples still demonstrate the profound effects migrations can have on communities and ecosystems. Changes in migratory behavior as a result of predation might thus have far-reaching consequences, especially if ecosystem functioning and biodiversity are dependent on migrations (Bauer and Hoye 2014). However, evidence for this remains limited (Figure 1). An exception to this is previously discussed roach. It has been shown that changes in migratory timing for the roach in Lake Krankesjön (the lake's main zooplanktivore) affects zooplankton community structure and abundance (Brönmark et al. 2014). Zooplankton grazing controls phytoplankton abundance, and with it the chance of clear water phases in spring. Spring clear water phases are crucial for the settlement of benthic macrophytes (Brönmark et al. 2014). As a result, changes in migratory timing could facilitate the transition from a clear lake with macrophytes to a turbid lake dominated by plankton (Brönmark et al. 2014). Predators can thus indirectly influence ecosystem structure through changes in migratory timing.

### Other possible consequences

Although I could find no direct evidence of ecological consequences of altered baleen whale migration and landscapes of opportunities for killer whales and sharks, these will undoubtedly have consequences. For example, the presence of large amounts of “fighting” baleen whales in near-shore calving grounds surely will impact the local ecosystem, for example through the vast amounts of food consumed and nutrients recycled (Savoca et al. 2021). The same goes for predation opportunities created by predictable mass migration of aquatic species. If predators alter their spatial distribution by following migrating species, this might reduce predation risk for other species. The predictable nature of some migrations might even cause some predator communities to become dependent on them.



Migrations may very well affect many other ecosystem, population and community aspects, such as altered gene flow, speciation, spread of invasive species (Bauer and Hoye 2014, Brönmark et al. 2014), etc. However as direct evidence for changes in such factors as a result of changes in migratory behavior in response to predation risk remains limited, I will not discuss them further. Altered spatial distribution through anti-predation responses can occur on smaller scales as well, which I will discuss in the following section.

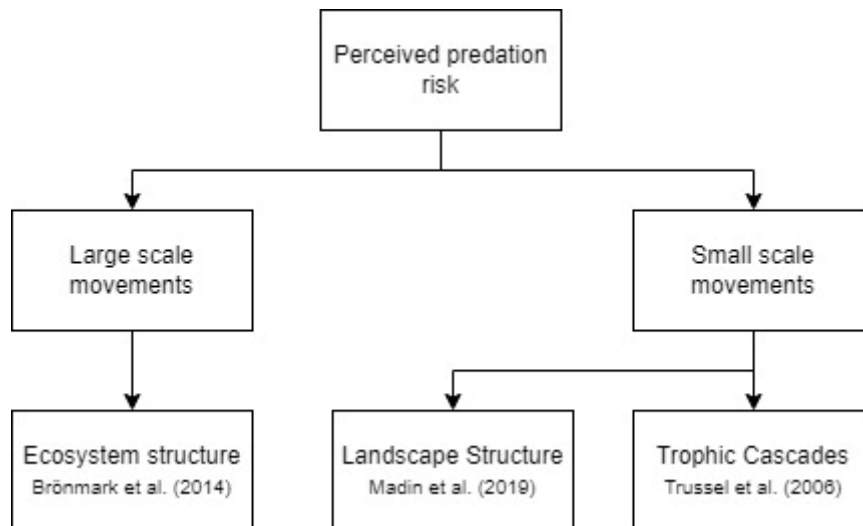


Figure 1: Diagram showing the studied direct ecological effects of altered movements in aquatic organisms due to perceived predation risk. Consequences may not be limited to the ones mentioned here, but this remains speculative without any direct evidence. Also see Table 1.

Table 1: An overview of evidence for altered spatial use of aquatic organisms in response to predation risk on various scales. Rows in **bold** are studies with direct evidence for ecological consequences of this altered spatial use as a response to predation risk.

Scale	Findings	Species	Scientific Name	Reference
Migration	Increased propensity to migrate under direct predation risk, and earlier departure under indirect predation risk.	Roach	<i>Rutilus rutilus</i>	Hulthén et al. (2015)
Migration	Predation risk likely shape migratory routes.	Baleen Whales	6 Species from Mysticeti	Ford and Reeves (2008)
Migration	No increased risk avoidance behavior under risk of predation.	Loggerhead turtles	<i>Caretta caretta</i>	Hammerschlag et al. (2015)
<b>Migration</b>	<b>Changes in migratory timing altered plankton communities, and may therefore alter stability of alternate stable states.</b>	<b>Roach</b>	<b><i>Rutilus rutilus</i></b>	<b>Brönmark et al. (2014)</b>
Emigration	Organisms emigrate from areas with high predation risk.	Grousewinged backswimmers	<i>Notonecta undulata</i>	Baines et al. (2015)
Emigration	Increased predation risk when dispersing leads to lower dispersal rates.	Daffodil cichlid	<i>Neolamprologus pulcher</i>	Groenewoud et al. (2016)
Between habitat distribution	Dolphins moved to less food-rich, but safer habitats.	Bottlenose dolphin	<i>Tursiops aduncus</i>	Heithaus and Dill (2002)
Between habitat distribution	Habitat use deviated from expected as predicted by a mathematical model.	Harbor seal	<i>Phoca vitulina</i>	Frid et al. (2007)
Between and within habitat distribution	Dugongs altered their vigilance, within habitat and between habitat distribution.	Dugong	<i>Dugong dugon</i>	Wirsing et al. (2008)
Within habitat distribution	Dolphins foraged around seagrass meadow edges instead of productive meadow interior.	Bottlenose dolphin	<i>Tursiops aduncus</i>	R. Heithaus and M. Dill (2006)
Within habitat distribution	Within habitat use is dependent on available alarm cues and predator species.	Roach	<i>Rutilus rutilus</i>	Martin et al. (2010)
<b>Within habitat distribution</b>	<b>Reduced foraging in risky habitats and increased foraging in safer habitats of an intermediate consumer led to trophic cascades.</b>	<b>Dog whelk</b>	<b><i>Nucella lapillus</i></b>	<b>Trussell et al. (2006)</b>
<b>Within habitat distribution</b>	<b>Various species preferred to feed close to protective reefs, creating unvegetated halos around reefs.</b>	<b>Various species of fish and sea cucumbers</b>	<b>Species from families Acanthuridae, Siganidae, Labridae, Haemulidae Lethrinidae, and from class Holothuroidea</b>	<b>Madin et al. (2019)</b>

## Small scale movements

### Predation-induced altered between and within habitat distribution

#### Anti-predator behaviors on various scales

While some species migrate to safer environments for prolonged periods of time, many species adjust their spatial distribution in response to perceived predation risk by moving between nearby habitats or within the same habitat for shorter periods of time (Table 1). For example, dugongs (*Dugong dugon*) alter their habitat use under tiger shark (*Galeocerdo cuvier*) presence. Shark presence fluctuates with water temperature, and dugongs shift their behavior in response to tiger shark abundance. Dugongs respond on three different spatial scales (Wirsing et al. 2008, Wirsing and Ripple 2011). On the finest scale, dugongs alter their foraging strategy. Dugongs prefer to forage in shallow seagrass meadows, and can either uproot seagrass, or crop it. Excavating seagrass yields more energy, but comes at the cost of vigilance due to the head-down posture of the dugongs (Wirsing et al. 2008, Wirsing and Ripple 2011). Moreover, uprooting seagrass creates clouds of sediment which may attract predators. When tiger shark presence in seagrass meadows is high, dugongs will shift their fine-scale foraging strategy from excavation to cropping. On a larger scale, dugongs alter their within habitat distribution. Tiger shark presence is highest around the peripheries of shallow seagrass meadows. In response, dugongs show a small-scale (tens of meters) shift in habitat use in a somewhat surprising manner: the dugongs will mostly forage around these meadow edges when predation pressure is high, sacrificing food from the internal meadow. Apparently, the opportunity to escape from the shallow meadow edge into deeper waters outweighs the risks of encountering more predators (Wirsing et al. 2008, Wirsing and Ripple 2011). At the largest scale, dugongs alter their between habitat distribution. When tiger shark abundance is high, some dugongs sacrifice food that might be acquired in food-rich, shallow seagrass meadows, and seek refuge in the less food-rich, but safer deeper waters (Wirsing et al. 2008, Wirsing and Ripple 2011).

Other marine mammals show responses that are very similar to those of dugongs. For example, bottlenose dolphins (*Tursiops aduncus*) also prefer forage in seagrass meadows where tiger sharks are present. Alternatively, the dolphins can forage in deeper habitats where both food and predators are less abundant. According to ideal free distribution (IFD) theory, individuals should spread out so that all individuals can get equal amounts of food. Deviation from IFD could indicate that dolphins prefer foraging in safer deep habitats as opposed to shallow more dangerous habitats (Wirsing et al. 2008). (Heithaus and Dill 2002) followed dolphins during a three-year period, and found that during winter, when predation pressure was low, dolphins followed IFD, with more individuals foraging in shallow waters. However, when predation pressure was high, dolphins spent significantly more time in deeper waters (Heithaus and Dill 2002, Wirsing et al. 2008). When staying in the more seagrass meadows, the dolphins also preferred to forage around meadow edges as opposed to the productive, but dangerous interior meadow (R. Heithaus and M. Dill 2006, Wirsing et al. 2008).

Yet another marine mammal that showed similar behaviors is the harbor seal (*Phoca vitulina*). These seals face a complex tradeoff between various prey species and predators at different depths (Heithaus et al. 2007, Wirsing et al. 2008). A mathematical model predicted that net energy intake should be highest in deeper strata, but actual seal behavior deviated from these predictions, suggesting an anti-

predator response in the form of altered habitat use (Frid et al. 2007, Wirsing et al. 2008). Organisms will thus alter their habitat use on various scales under risk of predation.

### Individual differences

Individual differences may also play an important role in determining within habitat distribution of prey in response to perceived predation risk. Juvenile three-spined sticklebacks (*Gasterosteus aculeatus*) were caught from various environments within Navarro River, CA (Pearish et al. 2013). It was shown, among other things, that individuals from different environments showed consistent behavioral differences (also known as animal personalities). Moreover, diet analysis revealed that diets also differed between individuals, indicating that some individuals made use of different microhabitats. Despite the short temporal scale of this study, and the limited evidence for a correlation between behavioral types and diet (and thus use of microhabitats), there is still evidence for at least short-term deviations from random distribution (Pearish et al. 2013). Note that predation risk was actually not incorporated into this study, but it has been shown that organisms with different animal personalities respond differently to predation risk as well. For example, bolder individuals take more risk, and will thus likely seek out riskier, but more resource rich habitats (Hulthén et al. 2017). However, there is also evidence against individual differences being predictive for niche use, as personalities of common bullies (*Gobiomorphus cotidianus*) did not predict their habitat use or diet (Kerr and Ingram 2020). While still uncertain, individuals may distribute themselves differently depending on their personality under risk of predation.

### Predator species and available alarm cues

Differential habitat use in response to predation risk is also dependent on predator species and available cues (Figure 2). Since omnivory is seen all over the natural world, most prey species have to assess predation risk from multiple predator species. Roach are a common brackish and freshwater fish species in Europe, that is commonly preyed upon by various piscivores. In an experiment, (Martin et al. 2010) exposed juvenile roach to visual cues and/or olfactory cues of northern pike (a common ambush piscivore) and/or European perch (*Perca fluviatilis*, a common roving piscivore). They found that roaches prefer to remain in open habitats when exposed to olfactory cues and in structured habitats when exposed to visual cues for pikes. This was the other way around for perch. When exposed to both predators, individuals preferred an open habitat when exposed to either olfactory or visual cues. When exposed to both vision and olfactory cues, the roach always preferred the structured habitat. This anti-predator response might be explained by foraging behavior of predators and uncertainty on where an attack will come from. For example, when a roach detects (but does not locate) an ambushing pike in a structured environment through olfactory cues, it will move to an open habitat to locate the predator. When a roach locates a pike in an open habitat, it will use the structured habitat as a defense (Martin et al. 2010). Changes in habitat dispersal may thus be dependent on predator species and environmental conditions.

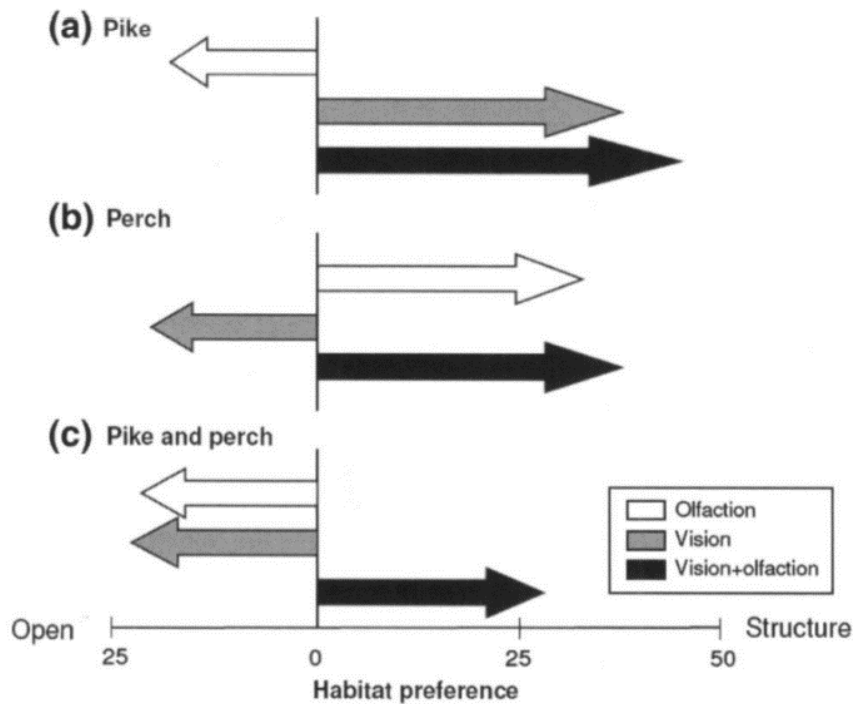


Figure 2: Conceptual diagram showing roach preference for different habitats for different alarm cues (olfactory and/or visual) and different predators (pike and or perch). Arrow length indicates the strength of preference (Martin et al. 2010).

## Ecological consequences of altered distribution within and between habitats

Many species interactions are determined by spatial-temporal distribution of individuals (Owen-Smith 2015). Changes in habitat use due to perceived predation risk might thus alter ecological interactions, with possible far-reaching consequences. For example, Bluegill sunfish (*Lepomis macrochirus*) are freshwater fish that either forage in the littoral zone or in open water, based on individual preference. Bluegill sunfish feeding in open water habitats can prevent other species, such as, pumpkinseeds (*Lepomis gibbosus*), from entering that niche. Moreover, bluegill sunfish encounter different predators and parasites in different habitats, as revealed by their difference in parasite load (Wolf and Weissing 2012). This type of habitat specialization could lead to lower selection pressure, which could maintain high variation in habitat use, and might even lead to reproductive isolation and speciation in the long term (Pearish et al. 2013). While these changes in habitat distribution may not necessarily have been the result of predation risk, this example still demonstrates how a change in habitat use might have extensive effects on species interactions.

## Trophic cascades

Direct evidence of altered species interactions as a result of altered habitat use in response to perceived predation risk is surprisingly scarce (Figure 1). However, in one study, it was shown the foraging of intermediate consumer (the carnivorous snail *Nucella lapillus*) was significantly suppressed under risk of predation by European green crabs (*Carcinus maenas*) (Trussell et al. 2006). Moreover, snails sought significantly more spatial refuge when crabs were present. The basal resource (the barnacle *Semibalanus balanoides*) increased by up to 580% in risky habitats, and decreased by 85% in refuge habitats as a result. The indirect cascading effects of predation (i.e. through anti-predator defenses) were as strong, if not stronger than direct lethal effects (i.e. density dependent) effects (Trussell et al. 2006).

## Landscape structure

Changes in habitat use can also lead to pattern formation. For instance, in coral reefs, herbivore fish graze away algae. The further the herbivores move away from the protective reef, the higher their predation risk. This predation risk differs between species, as larger bioturbating fish are found farther away from the reef (Madin et al. 2019). More immobile species (such as sea cucumbers) cannot escape from predators and will ignore predation risk altogether, preferring to graze wherever food density is highest. As a result of this risk-gradient, most species feed close to the protective reef (Madin et al. 2019). This leads to the formation of un-vegetated bands or “halos” around reefs. These halos are found all over the world. When predators are absent, for example under heavily fished conditions, these halos disappear (Madin et al. 2011). Altered species distribution as an anti-predator response can thus shape landscapes.

Patterns, such as the halos found around reefs (Madin et al. 2011, 2019), are found all over the natural world, and self-organized patterning resulting from ecosystem interactions have furthermore been found in a wide range of ecosystems (e.g. van de Koppel et al. 2008). It has been demonstrated that patterning can increase ecosystem resilience, stability and biodiversity (Liu et al. 2014). The presence of halos might have a variety of other effects (Madin et al. 2019). For example, halo formation with hard-bottom substrate could affect coral recruitment, as grazing of algae reduces competition, while scraping of corals by fish may simultaneously reduce coral recruitment. Moreover, benthic algae play an important role in a variety of ecosystem processes, such as stabilization of sediment and nutrient cycling, and the selective grazing thereof could thus have a variety of ecological impacts (Madin et al. 2019).

## Other consequences

There might be a variety of other consequences of altered non-random spatial distribution. For example, changes in foraging behavior and habitat use of dugongs might impact their seagrass resource. When predation risk is high, dugongs will excavate less seagrass, which could lead to a shift from annual to perennial seagrass species, or a different change in meadow species composition (Wirsing et al. 2008), as seagrass that would normally be consumed and excavated by dugongs might survive. Shape and size of seagrass meadows might also change with increased grazing pressure from dugongs along meadow edges. Moreover, the more frequent use of safer, impoverished habitats under high perceived predation risk will likely benefit plants in dangerous habitats, and harm plants in safer habitats (Wirsing et al. 2008). There will likely be a plethora of other ecological and evolutionary consequences of altered

spatial distribution in response to predation, but as actual evidence for such consequences remains scarce, I will not discuss them any further.

## Discussion

I have provided a general overview on how perceived predation risks alters spatial distribution of prey, and its consequences. Anti-predator defenses are seen all over the natural world, including aquatic environments. On a large scale, species might alter their migration propensity, paths or timing in response to increased predation risk or depending. In some cases, individuals may emigrate or actually delay dispersal due to high predation risk. Highly mobile species might adjust their migratory behavior, as predation risk is unpredictable. On a smaller scale, a variety of marine mammals switched their within and between habitat distribution and foraging strategies to reduce risk of capture. Roach also adjusted their spatial distribution based on alarm cues and predator species. Animal personalities may play a role in anti-predator responses as well.

The resulting changes in distribution as a result of anti-predator responses might have far-reaching effects ranging from the individual to the ecosystem. Migrations in themselves, and thus also changes in migratory behavior, can have massive consequences on the ecosystem. For example, changes in roach migration may lead to a shift from macrophyte dominated to plankton dominated waters. On a smaller scale, reef fish preferred to forage close to protective reefs, which led to the formation of patterns in the landscape, and altered habitat use of an intermediate consumer led to a trophic cascade. However, many of consequences of non-random distribution of organisms as a result of predation risk remain speculative, as direct evidence for ecological and evolutionary consequences of anti-predator defenses remain limited, both for larger scales (but see Brönmark et al. 2014) and smaller scales (but see Trussell et al. 2006, Madin et al. 2019).

One interesting way through which we may investigate this is by comparing aquatic and terrestrial ecosystems, as their landscapes of fear may actually be quite similar (Figure 3). While research is still limited, Wirsing and Ripple (2011) found that anti-predator behavior from dugongs in response to tiger sharks, and elk (*Cervus elaphus*) response to wolves showed some striking similarities. As described previously, dugongs respond to predation risk on three different scales: a fine scale shift from excavating of seagrass to cropping to remain more vigilant; a small scale shift to seagrass meadow edges to facilitate escapes; and a larger scale shift from risky, bountiful habitats to safer, more impoverished habitats to avoid predators. In terrestrial ecosystems, elk vulnerability is exacerbated by terrain features that impede their escape or limit their vigilance. Just like dugongs, elk respond to predation risk on three different scale: on the fine scale, elk increased their vigilance when near escape impediments; on a small scale, elk avoid sites with aspen (*Populus tremuloides*) near streams where logs impede escape; and on large scale, elk move from high quality grasslands monitored by wolves to coniferous forests in order to avoid predator encounters. So, in response to predation risk, both elk and dugongs reduce their foraging to increase vigilance, and alter their use of habitats to facilitate escape and avoid predators (Wirsing and Ripple 2011).



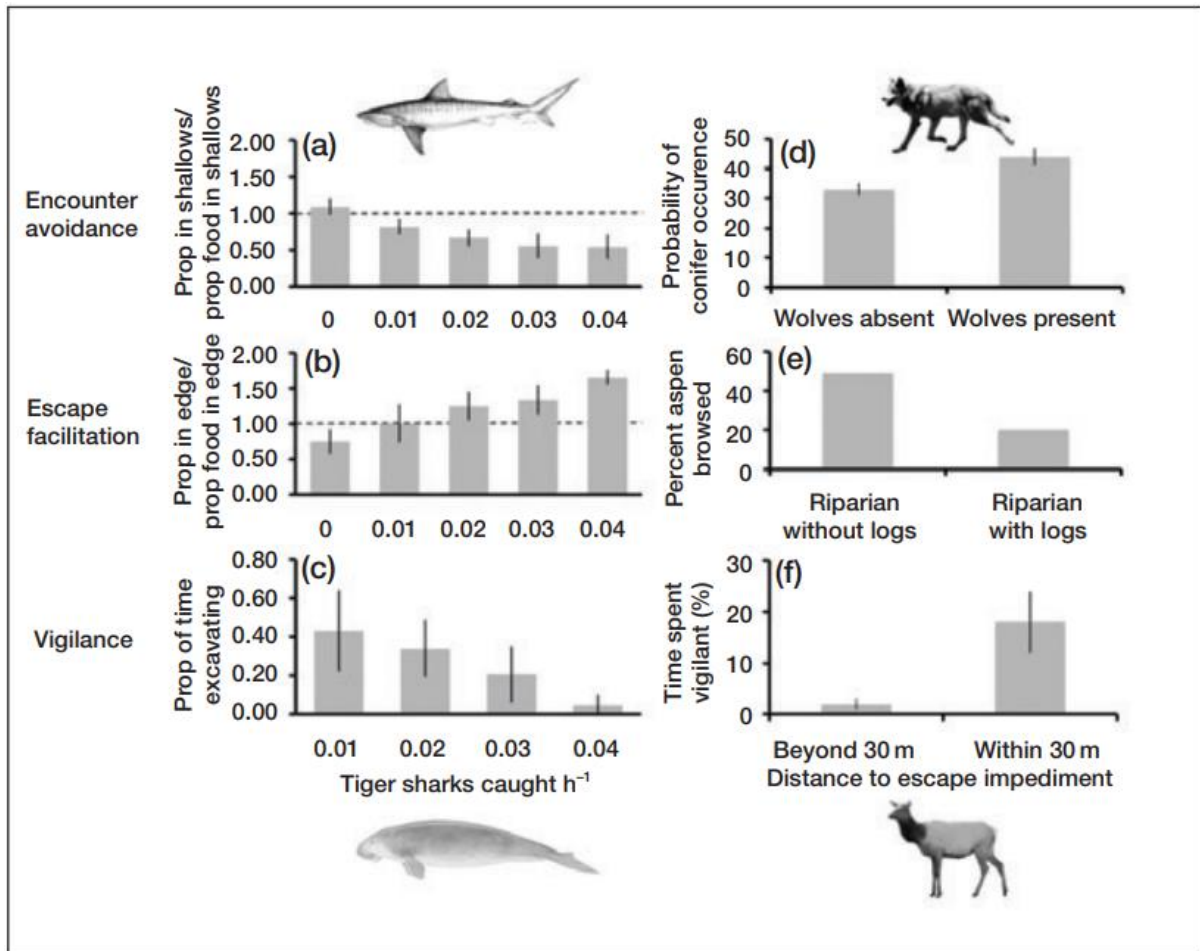


Figure 3: Figure showing the similarities in anti-predator response for aquatic and terrestrial systems. Both dugongs (left) and elk (right) alter their behavior on three different scales when predation risk is high. On a small scale, both species become more vigilant. On a larger scale, both species use habitats differently to facilitate their escape. On the largest scale, both species move between different habitats to reduce predator encounters.

Similarities may not be limited to just vigilance and habitat use. For example, large mixed elk herds drastically decreased in size in response to wolf presence. Smaller bull herds only slightly decreased in size. Both groups eventually converged to a similar size, which is probably the result of a predation dilution-detectability trade-off (Winnie and Creel 2007). While not sex-specific, Trinidadian guppies also decreased their group size in response to predation (Heathcote et al. 2017). Energetic state may also play an important role. During winters, female elk showed increased vigilance behavior in response to wolf presence. In contrast, males did not show this increased vigilance behavior, as they could not afford to reduce their food intake due to their poor energetic state (Winnie and Creel 2007). In marine habitats, green sea turtles (*Chelonia mydas*) preyed by tiger sharks selected profitable but risky habitats when their body condition was poor, while individuals in good condition selected safer, but less profitable habitats (Heithaus et al. 2007). Of course, many other similarities may be found between aquatic and terrestrial landscapes of fear, for a wide variety of terrestrial and aquatic species.

Scientific literature on spatial distribution of (aquatic) organisms is vast (e.g. Bauer and Hoye 2014, Brönmark et al. 2014, Schirmer et al. 2019). Due to temporal limitations, I have only had the chance to scratch the surface of this subject. For instance, anthropogenic disturbances are known to alter anti-predator behavior as well. In one study it was shown that road salt contamination can influence population dynamics in freshwater landscapes of fear. Acoustic disturbance also interferes with anti-

predator behaviors in some species (Spiga et al. 2017). Moreover, climate change may also interfere with anti-predator responses, as organisms reared in waters with high CO<sub>2</sub> concentrations displayed a slower, or even opposite response (i.e. an attraction) to alarm cues (Munday et al. 2016). Moreover, individual variations in anti-predator defenses could influence meta-population dynamics and range expansion for organisms, as well as a variety of other factors (Nilsson et al. 2014). While this was touched upon very briefly, a more complete overview was outside the scope of this essay. Nevertheless, this would make for an interesting topic for future research, especially because animal personalities are known to have a wide variety of ecological and evolutionary consequences (Wolf and Weissing 2012).

In conclusion, landscapes of fear are complex systems dependent on a variety of biotic and abiotic factors, in which anti-predator responses can have major consequences. However, direct evidence for these consequences is surprisingly limited, especially for aquatic ecosystems. Therefore, I think it is time to take a deeper dive into the matter, so we may better understand the non-lethal effects predators have on the ecosystem.

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