Oil exposure impairs predator–prey dynamics in larval red drum (Sciaenops ocellatus)

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Abstract. The 2010 Deepwater Horizon (DWH) oil spill in the Gulf of Mexico was the largest spill in recent history and led to the exposure of many commercially and ecologically important fish species. Crude-oil exposure is known to result in compromised cardiorespiratory function and swim performance of fishes, presumably altering ecological performance by impairing the ability to capture prey or evade predators. However, this has yet to be empirically tested. This study assessed the impacts of oil exposure on thigmotaxis (avoidance of exposed areas), routine activity, and prey-capture ability in larval red drum (Sciaenops ocellatus) by using environmentally relevant concentrations of weathered-oil water-accommodated fractions (0–55.9 µg L⁻¹ of total polycyclic aromatic hydrocarbons, ΣPAH). Oil exposure caused a dose-dependent increase in time spent in the exposed area of the arena, with an average three-fold increase at the highest dose, suggesting increased risk-taking. Although increased risk-taking resulted in 14% more area explored, oil-exposed individuals were significantly slower to catch prey and caught 67% less prey overall. Prey-capture ability did not appear to be related to cardiorespiratory or swimming impairments, because oil-exposed fish exhibited routine swim speeds and the distance travelled similar to those of the control, suggesting an alternate route of toxicity, such as cognitive impairments.

Additional keywords: Deepwater Horizon, development, oil spill, PAH, predator–prey interactions.

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Introduction

In 2010, the Deepwater Horizon (DWH) oil spill released ~4 million barrels (~700 GL) of crude oil into the northern Gulf of Mexico (Reddy et al. 2012), which coincided with the spawning season and hatching of many economically and ecologically important fish species (Rooker et al. 2013). Polycyclic aromatic hydrocarbons (PAHs) found in oil are well known toxicants in fish (see reviews by Collier et al. 2004; Buskey et al. 2016), and early life stages of pelagic marine fishes are particularly susceptible, with 50% lethal concentration (LC₅₀) values being reported to be in the low microgram-litre range (e.g. Esbaugh et al. 2016; Khursigara et al. 2017). Furthermore, oil exposure can also lead to sublethal cardiac defects, including increased incidence of malformation (Hicken et al. 2011; Edmunds et al. 2015), increased pericardial oedema (Incardona et al. 2004; Mager et al. 2014; Esbaugh et al. 2016), arrhythmia and bradycardia (Incardona et al. 2014), as well as overall reductions in contractility (Incardona et al. 2014; Esbaugh et al. 2016) and cardiac output (Nelson et al. 2016; Khursigara et al. 2017). These sublethal effects, in combination with shifts in primary production, predation and disease after oil spills, lead to difficulty predicting immediate and long-term responses of fish populations (Fodrie et al. 2014). Despite the well-known detrimental effects of oil on cardiorespiratory function, the ultimate significance of sublethal cardiac impairment in fish is less clear, particularly as it relates to animal ecology.

Studies of whole-animal performance have focused primarily on the aerobic and swimming capabilities of oil-exposed individuals. Several studies have demonstrated oil-induced impairment of critical swimming speed (Uₘ₉), maximum metabolic rate, and aerobic scope (Claireaux et al. 2004; Davoodi and Claireaux 2007; Hicken et al. 2011; Mager et al. 2014; Stieglitz et al. 2016; Johansen and Esbaugh 2017; Pan et al. 2018). It is generally believed that any reduction in Uₘ₉ and aerobic scope will coincide with reduced ecological performance, because these two measures represent the maximum capacity for exercise and activity. As such, it would be hypothesised that these oil-induced impairments would limit an individual’s ability to capture prey, evade predators, and effectively compete for resources in the environment, ultimately leading to ecological death. However, to our knowledge, this hypothesis has not been empirically tested.

More recent work has demonstrated that fish may also exhibit non-cardiac impairments that can have ecologically significant consequences. A recent study on coral-reef fish demonstrated that a 24-h oil exposure containing 5.7 µg L⁻¹ of ΣPAH₅₀ resulted in significant changes in habitat
utilisation, shoaling proclivity and predation exposure, all being behaviours that are typically associated with higher-order cognitive functions (Johansen et al. 2017). Overall, this led to an ~20% reduction in survival when exposed to a larval predator, relative to non-exposed individuals. Similarly, transcriptomic studies exploring the effects of oil on larval development in red drum (S. ocellatus) and mahi mahi (Coryphaena hippurus) have demonstrated oil-induced mRNA expression patterns consistent with abnormal neuro-functional logic (Xu et al. 2016, 2017). This leads to the hypothesis that, in addition to cardiac impairments, oil exposure of fish larvae can also alter behaviours that are critical for survival, such as risk-taking and prey-capture ability.

On this background, the current study sought to explore the potential effects of oil exposure on risk behaviour and prey-capture ability in red drum larvae (Sciaenops ocellatus). The red drum is an economically important species native to the coastal regions of the Gulf of Mexico and south-eastern United States and is a particularly relevant study species in the context of the Deepwater Horizon oil spill. An open-field test was used to assess changes in thigmotaxis (i.e. wall-hugging) in a novel environment as an indirect measure of predation risk-taking, which will be hereby referred to as risk-taking behaviour. Thigmotaxis is a measure of anxiety behaviour defined by the proclivity to remain near the perimeters of an arena or avoidance of the centre, and has been applied in many studies using rodents and fish to assess behaviours influencing predator and foraging function (Treit and Fundytus 1988; Champagne et al. 2010; Hamilton et al. 2017). Although no predator is introduced in this experiment, if fish spend more time in the open, exposed area of the arena, that could translate into greater predation risk in the wild. In addition, distance swam and total area of the arena explored were measured to indirectly investigate foraging opportunity on the basis of distance travelled. Prey capture was directly measured using a controlled assay that assessed time to capture and total prey items consumed in a given time frame.

**Materials and methods**

**Animal husbandry**

All experiments were approved by the Institutional Animal Care and Use Committee (IACUC) at the University of Texas at Austin. Newly fertilised red drum (Sciaenops ocellatus) embryos were obtained from broodstock tanks at the Texas Parks and Wildlife CCA Marine Development Center in Corpus Christi, Texas, USA. Embryos were treated with 1 g L⁻¹ formalin for 1 h, followed by three rinses with UV-filtered sterile seawater (35 ppt), after which they were stocked for rearing in 165-L conical tanks equipped with constant aeration and biofiltration. Embryos were reared in these tanks until experimentation. Feeding consisted of enriched rotifers (3–10 days post-fertilisation, DPF), followed by enriched *Artemia* nauplii. All tanks were maintained at 25°C. Larvae used were 21–35 DPF and 0.62–0.93 ± 0.03 cm (total body length).

**Oil exposures**

Oil-exposure concentrations spanning 0–55.9 µg L⁻¹ ΣPAH (control, low dose = 12.9, medium dose = 24.7–28.2, high dose = 47.8–55.9 µg L⁻¹ ΣPAH) were generated using high-energy water-accommodated fractions (HEWAFs), which were produced according to previously described methodology (Khursigara et al. 2017). All seawater (35 ppt) was autoclave-sterilised before use. HEWAFs were generated from a naturally weathered slick oil (referred to as OFS) obtained after the DWH spill from the Gulf of Mexico on 19 July 2010 from the hold of barge number CT02404. Oil samples were delivered to the University of Texas Marine Science Institute under proper chain of custody, and stored at 4°C. All larval exposures were conducted for 24 h in 400-mL glass beakers containing 325 mL of spiked seawater. The HEWAF spiked seawater was generated in 3-L volumes and allowed to mix for 5 min with a 25% vortex. An initial 250-mL water sample was taken from each concentration and sent to ALS Environmental (Kelso, WA, USA) on ice for determination of ΣPAH concentrations. PAHs were extracted under protocol EPA 3510C and measured according to protocol 8270D SIM. Samples were spiked with fluorine-d10, fluoranthene-d10 and terphenyl-d14 to assess extraction efficiency, with general recovery of >80, >90 and >90% respectively. Detection limits ranged from 4.5 to 20.5 ng L⁻¹, depending on the specific PAH. All samples were stored at 4°C and delivered within 1 week of collection. Exposures were conducted in an incubator that maintained water temperature at 25°C, with a photoperiod of 14 h light: 10 h dark. No food was introduced during exposures and each replicate was lightly aerated. Immediately after the 24-h exposure, larvae were removed from spiked seawater and transferred by net to their respective testing arena for acclimation. Water-quality parameters, including dissolved oxygen, pH, salinity and temperature, were monitored at the beginning and end of each exposure.

**Open-field assays**

Open-field thigmotaxis and routine foraging activity was conducted using 21-DPF larvae exposed to control, 24.7 or 47.8 µg L⁻¹ ΣPAH (n = 16). Note that no 12.9 µg L⁻¹ treatment was included for open-field assays because of the availability of larval red drum. Each individual fish was removed from its respective treatment water and transferred by net to a 15-cm-diameter (~15 body lengths) circular chamber filled with 75 mL of clean seawater. A shallow depth of 3 cm was maintained to limit vertical movement. The test occurred in a dark room with the field arena backlit and enclosed by a black box to eliminate external disturbance. After 1 h of acclimation, swimming activity was recorded for 15 min with a 3 uEye camera (IDS Imaging Systems, Obersulm, Germany) mounted above the field arena. Owing to the fish’s small size (1 : 3000 fish-to-volume ratio) and large surface area of the arena, oxygen depletion was presumed to be negligible. Videos were analysed for thigmotaxis and total swimming distance using Ethovision XT (ver. 8.0, Noldus, Leesburg, VA, USA) tracking software. Thigmotaxis was calculated by defining an inner and outer zone, where the inner circular zone equalled half the area of the entire field arena (Hamilton et al. 2017). Data are represented as the percentage of time spent in the inner, or higher-risk, zone. The spatial area explored by the fish was assessed manually by using ImageJ (ver. 1.8, National Institutes of Health, Bethesda, MD, USA). The arena was divided into 1-cm² grids, and the total
number entered by the fish, as defined by centre body length, was recorded.

**Prey-capture assays**

Prey-capture assays were performed with 35-DPF larvae exposed to control, 12.9, 28.2 or 55.9 μg L⁻¹ ΣPAH (n = 16). Prey-capture assays were conducted with different larvae than were the open-field assays because of fast growth and 35-DPF larvae were used as opposed to 21-DPF because of a larger size (~0.5 cm). Each individual fish was removed from its respective treatment water, transferred to a test arena, and allowed to acclimate for 30–60 min. The test arena consisted of a 100-mL glass beaker filled to a depth of 2.5 cm (40 mL) with seawater. Upon acclimation, 10 Artemia nauplii were introduced to the centre of the arena by using a plastic pipette, and the time to 1st, 5th and 10th capture was recorded. The test was terminated after 10 min, and the total number of uneaten Artemia, if any, was recorded. Few individuals, oil-exposed or control, were able to capture all 10 prey items in the allotted 10 min, thus time to 10th capture is not included in the results.

**Statistics**

The effects of oil on thigmotaxis, total swimming distance and area covered were tested by comparing against the control group by using a one-way ANOVA followed by post hoc Tukey tests for specific differences for each exposure concentration. Prey capture was analysed using a one-way ANOVA on ranks, followed by Dunn’s post hoc test. Homogeneity of variance was analysed using Bartlett Chi-Square, and normality was assessed using visual plots. Coxbox transformations were applied where necessary to comply with assumptions. All analyses were conducted using SigmaPlot (ver. 13.0, Systat Software, Inc., San Jose, CA, USA) and Statistica (ver. 13, Dell Inc., Round Rock, TX, USA).

**Results**

**Chemical analysis of HEWAFs**

The relative abundances of specific PAHs found within the exposures are shown in Fig. 1. As expected for a weathered oil, the three-ring PAHs were the most abundant chemical class, making up 69.0 ± 0.3% (n = 7 measurements) of the measured ΣPAH₅₀. The second-most abundant class was the four-ring PAHs, which accounted for 26.1 ± 0.3% of the measured ΣPAH₅₀, and the remaining classes accounted for <5%. There was no significant change in water-quality parameters after oil exposure.

**Open-field assays**

Oil exposure had a significant effect on thigmotaxis across all exposure concentrations examined ($F_{2,43} = 4.52$, $P = 0.02$), causing individuals to spend more time in the exposed, open area of the test arena. Whereas control individuals entered the inner section of the arena only 6.7 ± 1.9% of the time, individuals exposed to 24.7 and 47.8 μg L⁻¹ ΣPAH occupied this area 20.1 ± 6.0% ($P = 0.03$) and 18.4 ± 4.4% ($P = 0.04$) of the time respectively (mean ± s.e.m., Fig. 2a). Across all doses, oil-exposed red drum (S. ocellatus) showed no change in relative swimming distance or speeds when compared with the controls ($F_{2,43} = 0.92$, $P = 0.41$, Table 1), but did significantly increase the total area explored ($F_{2,43} = 6.64$, $P < 0.01$). Individuals exposed to 47.8 μg L⁻¹ ΣPAH demonstrated a significant 14.2 ± 2.1% increase in area explored within the test arena ($P < 0.01$; Fig. 2b).

**Prey-capture assays**

Oil exposure resulted in a dose-dependent decrease in the total number of prey eaten ($H_S = 12.014$, $P = 0.007$), with a significant decrease after exposure to 55.9 μg L⁻¹ ΣPAH compared with the control ($P = 0.003$; Fig. 3a). Time to 1st and 5th capture increased in a dose-dependent pattern after oil exposure, with a significant increase in time to 5th capture ($H_S = 15.609$, $P \leq 0.05$) and a nearly significant increase in time to 1st capture ($H_S = 7.253$, $P = 0.06$) after exposure to 55.9 μg L⁻¹ ΣPAH (Fig. 3b).

**Discussion**

Exposure to oil pollution is known to cause elevated mortality, developmental defects and reduced cardiorespiratory functioning in marine fishes (e.g. Incardona et al. 2014; Esbaugh et al. 2016; Johansen and Esbaugh 2017; Khursigara et al. 2017; Xu et al. 2017; Magnuson et al. 2018; Pan et al. 2018), yet associated ecological consequences remain uncertain. Here, we have demonstrated that oil exposure to environmentally relevant concentrations increases risk-taking behaviour and reduces prey-capture ability in larvae of the economically important red drum, S. ocellatus. The capacity to minimise predation risk (predatory avoidance and escape) and capture food is reliant on accurate sensory information and interpretation (Lima and Bednekoff 1999a, 1999b; Brown et al. 2008, 2011) and oil-driven changes to these critical performance characteristics may directly affect survival and productivity of affected individuals and populations, although the latter is more difficult to ascertain. Although there is mounting evidence of lethal and sublethal effects on an individual after oil exposure, many estuarine fishes in the Gulf of Mexico may have developed avoidance or compensatory strategies in response to the DWH spill (Fodrie et al. 2014; Claireaux et al. 2018). Furthermore, delayed responses (>2 years post-spill) in potentially affected populations make it increasingly difficult to accurately evaluate population-level effects.

When foraging or exploring new territory, small animals will typically avoid open areas devoid of shelter, for fear of predators and unknown dangers (Almany and Webster 2006). Accordingly, larval red drum unaffected by oil pollution engaged in greater thigmotaxis and stayed close to the wall of the arena in an unfamiliar environment, and only transiently (<7% of the time) entered open areas with a potential higher risk of predation. Conversely, individuals exposed to 24.7 μg L⁻¹ ΣPAH were more than three times as likely to stray from the perimeter of the arena, spending, on average, 20.1% of the time in the higher-risk centre of the arena (Fig. 2). Thigmotaxis (i.e. wall-hugging) has been extensively used as an indicator of anxiety in many animals including fish (Schnörr et al. 2012), and here provides a clear indication of a significantly altered ability to either perceive or assess risk...
Fig. 1. The relative polycyclic aromatic hydrocarbon composition of naturally weathered slick-oil (OFS) high-energy water-accommodated fractions. Data represent mean ± s.e.m. of measurements across all dilutions (n = 7).

Fig. 2. Time in inner zone and total area explored by larvae of *Sciaenops ocellatus* 21 days post-fertilisation (DPF). (a) Risk-taking behaviour as the percentage of time individuals spent in the open centre of the arena. (b) The area explored as a percentage of total arena area. Oil concentrations are expressed as the initial sum of polycyclic aromatic hydrocarbons (ΣPAH). Error bars are s.e.m. and significant differences relative to control are highlighted with asterisks (P ≤ 0.05; n = 16).

Table 1. Mean swimming distance and swimming speeds of larval red drum

Distances swam are presented relative to body length over a 15-min period, whereas swimming speeds are in body lengths per second. Oil-exposure concentrations are expressed as the initial sum of polycyclic aromatic hydrocarbons (ΣPAH). Error terms are s.e.m.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Concentration (µg L⁻¹ ΣPAH)</th>
<th>0</th>
<th>24.7</th>
<th>47.8</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance swam (body lengths)</td>
<td>2618 ± 212</td>
<td>2163 ± 233</td>
<td>2407 ± 253</td>
<td></td>
</tr>
<tr>
<td>Swimming speed (body lengths s⁻¹)</td>
<td>2.91 ± 0.24</td>
<td>2.40 ± 0.26</td>
<td>2.67 ± 0.28</td>
<td></td>
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</tbody>
</table>
following oil exposure. Importantly, a loss of sensory capacity, such as the lateral line system or visual acuity, would not only affect the ability to perceive risk but also the ability to swim or manoeuvre (e.g. Stewart et al. 2017). All individuals swam readily, and none were found to haphazardly hit obstacles (L. E. Rowsey, pers. obs.), suggesting that recorded behavioural changes were not related to major sensory defects.

Dangers associated with settlement in open areas away from shelter may be minimised by exploiting camouflage and avoiding unnecessary movements that attract attention (e.g. Johansen et al. 2017). This is the primary hunting strategy of many sit-and-wait predatory fishes (Preisser et al. 2007). Indeed, red drum is fairly well camouflaged for the sandy and muddy habitats typically occupied within the Gulf of Mexico (Gallaway et al. 2007; Mendelssohn et al. 2012), and settlement in open areas away from shelter may, therefore, not compromise chances of survival, as long as appropriate behavioural responses are elicited. Unfortunately, oil-exposed red drum individuals maintained the same degree of movement activity and swimming speed as did the control individuals, despite being situated in higher-risk open areas of the test arena. This strategy is likely to cause increased mortality (Johansen et al. 2017), but perhaps also increased foraging success if prey-capture ability remained unchanged.

Oil-exposed larvae were more exploratory and covered a larger total area of the open arena, which are behaviours that should have exposed these larvae to a greater number of potential prey items. Yet, prey capture showed a clear dose-dependent response to oil exposure, with exposed larvae taking longer to capture individual prey and catching fewer total prey than did unexposed controls. The greatest reductions in performance were recorded at the highest oil doses examined (47.8–55.9 μg L⁻¹ ΣPAH). Similar to risk assessment, the ability to capture prey is reliant on accurate sensory inputs, cognitive functions, and the basic ability to swim. Our study showed that individuals exposed to 47.8–55.9 μg L⁻¹ ΣPAH were still able to catch prey and were still maintaining the same routine swimming speeds as did the controls, highlighting that recorded reductions in prey-capture efficiency are most likely related to either sensory efficacy or other cognitive function. In addition, control larvae and oil-exposed larvae exhibited the same morphology, further suggesting reduced neurological function as the probable cause as opposed to physical malformities. Regardless of the specific pathway of impairment, the inability to capture prey effectively has severe immediate and long-term energetic disadvantages, including reduced investment into growth, reproduction and long-term viability.

It is interesting that even the highest oil exposures examined did not result in a reduced distance swim. It is well known that oil causes a significant reduction in respiratory performance and $U_{\text{crit}}$ (Davoodi and Claireaux 2007; Hicken et al. 2011; Claireaux et al. 2013; Mager et al. 2014; Nelson et al. 2016; Stieglitz et al. 2016), presumably owing to impaired cardiovascular function (Brette et al. 2014; Edmunds et al. 2015; Esbaugh et al. 2016; Nelson et al. 2016, 2017). Although aerobic metabolism and swim performance were not measured here, the doses used ($\geq 47.8$ μg L⁻¹ ΣPAH) are above those of previous work on varying life stages of red drum that have identified such impairments (2.2–4.1 μg L⁻¹ ΣPAH₅₀, Johansen and Esbaugh 2017; Khursigara et al. 2017). This would suggest that, although maximum performance may be affected by acute oil exposure, these effects do not extend to routine activity levels, such as those measured here.

Perception and evaluation of risk is typically considered a complex higher-order cognitive function (Lima and Bednekoff 1999a, 1999b; Brown et al. 2008, 2011), as are predictions of prey movement patterns (Brown et al. 2008). Altered behavioural responses related to increased risk-taking and social interactions were recently shown in oil-exposed coral reef fishes (Johansen et al. 2017), and were speculated to be caused by impaired higher-order cognitive functions. The basis for impaired cognitive functions as a consequence of oil exposure remains uncertain, but mechanistic evidence is growing. Studies exploring gene expression during development have recorded
oil-driven changes associated with sensory systems and neurological development (Carvalho et al. 2008; Xu et al. 2017, 2016), highlighting the possibility of alternative routes of toxicity in larval fishes. Although our results were unable to distinguish the underlying mechanism, it is clear that the sensory modality of oil-exposed individuals still appeared to be working, albeit with a lower acuity; namely, oil exposed red drum could still swim, locate prey and feed, although at a reduced efficiency. Furthermore, the increased risk-taking behaviour seems less likely to be the result of an impaired sensory system. Similar to the conclusion reached by Johansen et al. (2017), the most likely explanation for observed patterns relates to an impairment of the way in which the brain interprets sensory information and makes decisions.

Broader ecological impacts of the 2010 DWH oil spill are still widely unexplored, and current knowledge is primarily based around pelagic species, such as mahi mahi (Mager et al. 2014; Esbaugh et al. 2016; Stieglitz et al. 2016). Although the results of the present study are a robust demonstration that larval red drum exhibits altered behaviours of ecological significance following oil exposure, it is important to recognise the challenges of extrapolating laboratory exposures and behavioural assessments to field scenarios. The DWH oil spill was clearly a heterogeneous exposure scenario that occurred in combination with varying environmental conditions. Such scenarios are difficult to reproduce in a controlled fashion, and this becomes more challenging when exploring highly variable endpoints, such as animal behaviour. Yet it is important to remember that the current work is built on a solid foundation of mechanistic studies that have previously demonstrated a suite of physiological and morphological impairments in red drum following oil exposure (Johansen and Esbaugh 2017; Khursigara et al. 2017; Xu et al. 2017), as well as transcriptomic evidence that has indicated neuronal impairment (Xu et al. 2017). As such, the current study sought only to test the a priori hypothesis that environmentally relevant exposure concentrations (Diercks et al. 2010) would result in adverse outcomes on individual performance. Importantly, the reductions in prey capture and potential predator avoidance observed here are likely to have important ecological impacts on long-term productivity and viability of affected populations. Given that red drum is considered an extremely hardy species capable of withstanding harsh environmental conditions. Given that red drum is considered an extremely hardy species capable of withstanding harsh environmental conditions. Given that red drum is considered an extremely hardy species capable of withstanding harsh environmental conditions. Given that red drum is considered an extremely hardy species capable of withstanding harsh environmental conditions. Given that red drum is considered an extremely hardy species capable of withstanding harsh environmental conditions. Given that red drum is considered an extremely hardy species capable of withstanding harsh environmental conditions.

Conflicts of interest

J. L. Johansen is an Associate Editor for Marine and Freshwater Research. Despite this relationship, he did not at any stage have Associate Editor-level access to this manuscript while in peer review, as is the standard practice when handling manuscripts submitted by an editor to this journal. Marine and Freshwater Research encourages its editors to publish in the journal and they are kept totally separate from the decision-making processes for their manuscripts. The authors have no further conflicts of interest to declare.

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