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Review

The effects of ultraviolet radiation and climate on oil toxicity to coral reef organisms – A review

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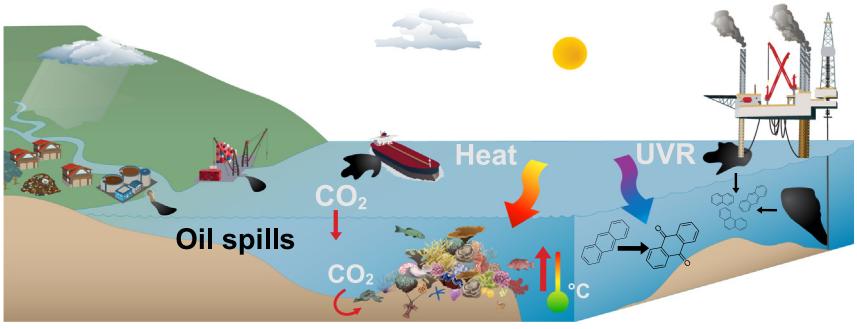
HIGHLIGHTS

- Oil pollution remains a threat to coral reefs and may interact with other pressures.
- A review was performed of the oil-multiple stressor literature for coral reef species.
- UV radiation, elevated temperature and low pH can increase the toxicity of oil pollutants.
- Further research is needed to assess impacts of tropical conditions on oil toxicity.
- UV radiation should be included as a standard co-factor in tropical oil toxicity testing.

GRAPHICAL ABSTRACT



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ABSTRACT

Oil pollution remains a significant local threat to shallow tropical coral reef environments, but the environmental conditions typical of coral reefs are rarely considered in oil toxicity testing and risk assessments. Here we review the effects of three environmental co-factors on petroleum oil toxicity towards coral reef organisms, and show that the impacts of oil pollution on coral reef taxa can be exacerbated by environmental conditions commonly encountered in tropical reef environments. Shallow reefs are routinely exposed to high levels of ultraviolet radiation (UVR), which can substantially increase the toxicity of some oil components through phototoxicity. Exposure to UVR represents the most likely and harmful environmental co-factor reviewed here, leading to an average toxicity increase of 7.2-fold across all tests reviewed. The clear relevance of UVR co-exposure and its strong influence on tropical reef oil toxicity highlights the need to account for UVR as a standard practice in future oil toxicity studies. Indeed, quantifying the influence of UVR on toxic thresholds of oil to coral reef species is essential to develop credible oil spill risk models required for oil extraction developments, shipping management and spill responses in the tropics. The few studies available indicate that co-exposure to elevated temperature and low pH, both within the range of current daily and seasonal fluctuations and/or projected under continued climate change, can increase oil toxicity on average by 3.0- and 1.3-fold, respectively. While all three of the reviewed environmental co-factors have the potential to substantially increase the impacts of oil pollution in shallow reef

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environments, their simultaneous effects have not been investigated. Assessments of the combined effects of oil pollution, UVR, temperature and low pH will become increasingly important to identify realistic hazard thresholds suitable for future risk assessments over the coming century.

Contents

1. Introduction

1.1. Petroleum hydrocarbons in coral reef environments

Petroleum hydrocarbons are considered among the most prominent pollution threats to marine environments (Islam and Tanaka, 2004; Haapkylä et al., 2007), and large oil spill events are of particular concern for habitats of high ecological importance, such as coral reefs. Recent examples of spills in the tropics and subtropics include the Deepwater Horizon crude oil spill in the Gulf of Mexico in 2010 (Diercks et al., 2010), the Montara wellhead oil spill on the North West Shelf of Western Australia in 2009 (AMSA, 2010), and the heavy fuel oil spilled from the bulk carrier *MV Solomon Trader* which grounded on a coral reef in the Solomon Islands in 2019 (Daley, 2019). While large spills and accidental discharges occur infrequently, their impacts can be catastrophic and last for decades (Jackson et al., 1989; Boehm et al., 2007; Beyer et al., 2016; Hook et al., 2016). For example, extensive mortalities of fish, corals, gastropods, bivalves, echinoderms, crustaceans and algae have been documented following oil spill events near coral reefs (Loya and Rinkevich, 1980; Jackson et al., 1989), with impacts on habitat forming species, such as reef-building corals, of particular ecological consequence (Keesing et al., 2018).

Each oil spill event is unique and the resulting toxic effects depend on the amount and type of spilled oil, how it was released, the location of- and conditions at the spill site as well as weathering and the spill responses employed (NRC, 2003; Haapkylä et al., 2007; Redman and Parkerton, 2015) (Fig. 1). Aromatic hydrocarbons, including monocyclic aromatic hydrocarbons (MAHs) and polycyclic aromatic hydrocarbons (PAHs) comprise only a small fraction of most petroleum oils and fuels, but these moderately water-soluble compounds are considerably more bioavailable and toxic to benthic and pelagic species than the insoluble aliphatic hydrocarbons (Di Toro et al., 2000; French-McCay, 2002). Organisms at the surface and in the intertidal zone can be affected by direct contact with whole oil and organisms in shallow water may also encounter oil droplets during a spill. However, the most frequently reported mode of action of petroleum pollution towards sub-surface aquatic taxa is non-polar narcotic toxicity, caused by the accumulation of dissolved aromatics in lipid membranes leading to disrupted cell integrity and homeostasis (Sikkema et al., 1995; Di Toro et al., 2000; Rougée et al., 2006; Zhu et al., 2008; Tarrant et al., 2014). Specific effects also include DNA damage (Shaw and Connell, 2001; Sarker et al., 2018) and oxidative stress (Wilk et al., 2013). All of these effects can compromise development or metabolism, and in some cases lead to mortality (Billiard et al., 2008). Most assessments of oil spill risks to benthic and pelagic marine species are therefore now based on oil spill trajectory and fate models and predictive toxicity models that include the expected exposure to, and hazards of, the dissolved aromatic fraction (French-McCay, 2002; French-McCay et al., 2018; McGrath et al., 2018).

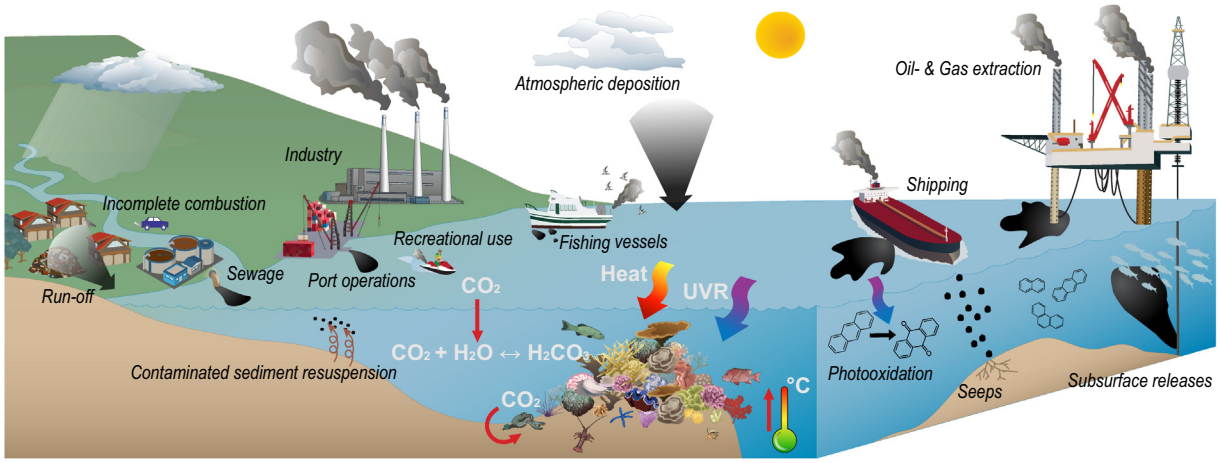

Fig. 1. Petroleum hydrocarbon sources and environmental factors affecting coral reef environments with potential for interacting effects on coral reef organisms. Sources of petroleum shown in black and environmental co-factors shown in white. Blue-purple radiation arrows indicates ultraviolet radiation exposure while red-orange arrow indicates heat from visible- and infrared radiation. Symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols). For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.

The direct exposure duration from spill events can be relatively short (hours-weeks); however, contamination of benthic reef habitats (Loya and Rinkevich, 1980) and depuration times for marine organisms can be long (Knap et al., 1982; Solbakken et al., 1983; Kennedy et al., 1989; Kennedy et al., 1992), resulting in potentially large windows for interactions with environmental factors (Fig. 1). Shallow coral reefs are routinely subjected to multiple environmental pressures, including high ultraviolet radiation (UVR) (Shick et al., 1996; Barron et al., 2009; Michael et al., 2012; Nordborg et al., 2018), high temperatures (Hoegh-Guldberg, 1999; Habary et al., 2016; Hughes et al., 2017), low pH (Hoegh-Guldberg et al., 2007; Doney et al., 2009; Price et al., 2012) and fluctuations in water quality parameters such as salinity, sedimentation and nutrients (Fabricius, 2005) (see also Fig. 1). For example, UVR (UVA: 320–400 nm and UVB: 280–320 nm) (Tedetti and Sempere, 2006; Banaszak and Lesser, 2009; Häder et al., 2015) is high throughout the year in tropical regions (0–30° latitude (Brown et al., 1994; Masiri et al., 2008)) and reaches significant depths in oligotrophic waters (>30 m) (Gleason, 2001; Banaszak and Lesser, 2009; Barron et al., 2009; Overmans and Agustí, 2019). Exposure to UVR can substantially increase oil toxicity (phototoxicity) through photosensitisation and photomodification (Barron, 2017; Roberts et al., 2017; Bridges et al., 2018) (see Section 2.2). High temperature (marine heatwaves) and low pH events (due to combined effects of local diurnal cycles and ocean acidification; OA) are projected to become more frequent and extreme with ongoing anthropogenic climate change (Hoegh-Guldberg et al., 2007; Habary et al., 2016; Hughes et al., 2018), potentially changing the vulnerability of coral reefs to the impacts of oil spills. The sensitivity of marine ectotherms to pollutants generally increases at temperatures approaching upper thermal tolerance ranges (Heugens et al., 2001) (Section 2.3), while less is known about the influence of low pH on the toxicity of organic contaminants (Section 2.4).

The combined and cumulative effects of pollutants and environmental pressures are increasingly recognised for their potentially compounding impacts on coral reefs (Ban et al., 2014; Zeng et al., 2015; Uthicke et al., 2016; Barron, 2017; Magris et al., 2018). While such multi-stressor effects have rarely been considered in the context of oil spills, French-McCay et al. (2018) recently recommended the application of a 10-fold safety factor on threshold values applied in oil spill risk assessments for subtropical species in the top 20 m of the Gulf of Mexico to account for phototoxicity. Predictive toxicity models with the capacity to account for phototoxicity are also under development (Marzooghi et al., 2016; Marzooghi et al., 2018) and some existing toxicity models can account for temperature differences through re-calculation of threshold values to a standardised temperature (French-McCay, 2002). However, the sensitivities of coral reef species to oil pollution are poorly understood, due to a focus on testing temperate species (French-McCay, 2002; Hook et al., 2016; McGrath et al., 2018), as well as methodological inconsistencies (e.g. lacking chemical analysis) associated with oil toxicity studies on tropical species (Haapkylä et al., 2007; Barron, 2017; Turner and Renegar, 2017; Keesing et al., 2018; Hodson et al., 2019). Therefore, the toxicity thresholds for oil-related contaminants applied in risk- and natural resource damage assessments may not be appropriate for coral reef species which regularly encounter environmental conditions that affect oil toxicity (Kwok et al., 2007; Barron, 2017; Forth et al., 2017; Bridges et al., 2018). As the use, transport and extraction of oil at sea is expected to continue over the coming century (PGM Environment, 2012; Wan and Chen, 2018), understanding the types and scale of interactions between oil pollution and environmental conditions (current and future) will be vital to inform the development of climate and UVR-adjusted hazard thresholds to improve water quality guidelines and risk assessments for oil pollution in coral reef environments.

1.2. Review scope and objectives

The decline of coral reefs globally (Bellwood et al., 2004; Pandolfi et al., 2011; De'ath et al., 2012) and their regular and increasing exposure to potentially interacting co-factors such as UVR, thermal stress and OA (Banaszak and Lesser, 2009; Hoegh-Guldberg et al., 2017; Hughes et al., 2018), raises the possibility that coral reefs may be particularly vulnerable to pollution from accidental oil spills. While there are many additional co-factors that may interact with the effects of oil pollution on coral reef environments they are beyond the scope of this review. The purpose of this review is to: (i) assess and quantify the influence of the environmental co-factors UVR, elevated temperature and low pH on dissolved hydrocarbon toxicity to pelagic and benthic coral reef organisms; (ii) identify important knowledge and data deficiencies on how environmental co-factors affect the sensitivity of reef organisms to petroleum hydrocarbons, and (iii) recommend research priorities and methodologies to improve toxicity testing for policy and guideline development relating to oil pollution in coral reef environments that account for relevant current, and future, UVR and climate conditions.

2. Impacts of environmental pressures on petroleum hydrocarbon toxicity to coral reef species

2.1. Literature identified for review

Searches of the ISI Web of Science database from 1980 to 2018 (search term: coral reef* oil) yielded 436 records of which 27 were experimental publications on the effects of petroleum hydrocarbons on coral reef associated organisms. This initial list of publications was supplemented using: (i) references from identified publications, (ii) publications of observed impacts from the field following spills, (iii) publications previously known to the authors and (iv) through additional, more specific searches of citation databases, the ISI Web of Science and Google Scholar (e.g. 'tropical fish oil pH'). Additional studies on species with tropical to subtropical distribution ranges that are associated with other marine habitats (as outlined in Tables A2-A4, Supplementary material A) were included for comparison where little or no information was available for the corresponding coral reef associated taxonomic group.

A total of 84 multi-stressor oil toxicity tests on tropical and subtropical species were identified (methods and results summarised in Table A2-A4), with 45% testing a total of 20 water accommodated fractions (WAF) of complex oil mixtures. Of these 37% used low energy preparations (WAFs), 51% high energy preparations (HEWAF) and 9% other solution preparation methods (Tables 1–2 and A2-A4). The remainder of the tests examined 25 individual petroleum compounds including the PAHs anthracene, phenanthrene, benzo[*a*]pyrene, fluoranthene and pyrene. 28 of the 84 tests used coral reef species (summarised in Tables 1–2), and reef-building corals were the most represented taxa (46%). Of the tests on reef species, 89% assessed ecologically relevant endpoints (mortality, growth, reproductive success and life stage transitions (Warne et al., 2018)), while the remainder assessed sub-lethal indicators of stress not currently considered ecologically relevant as defined in the national guidelines for water quality (Warne et al., 2018). However, only 36% of tests measured and reported concentrations of aromatics in tested solutions. No study co-exposed coral reef species to low pH and petroleum hydrocarbons. For brief summaries of publications testing the general toxicity of petroleum hydrocarbons towards coral reef species see Section 1 of Supplementary Material A. A summary of the influence of UVR, elevated temperature and low pH in all tests reviewed here can be found in Table 3, separated into coral reef species and benthic and pelagic species across all tropical marine habitats, respectively (for further details please see Tables A2-A4 of Supplementary materials).

Table 1
Summary of tests investigating the phototoxicity of petroleum hydrocarbons on coral reef organisms detailing experimental parameters and main results. Where multiple endpoints were assessed only results for the most sensitive endpoint were included (for consistency with Australian and New Zealand water quality guidelines as per Warne et al. (2018)). Exposure length shown in brackets, for further details on pollutants, test methodology and results please refer to Table A2, Supplementary material. Toxic threshold values presented as '-UVR to +UVR' where applicable. Unless specifically stated -UVR controls were utilised in experimental design. UVR irradiance for +UVR treatments reported as total UVA and UVB unless otherwise specified. Measured concentrations reported if available. Species and life stage: A = adult, L = larvae. UVR treatment: A = artificial UVR, S = ambient solar UVR. No -UVR = no -UVR control used in experiment. Toxicity: Meta. = metamorphosis, No phototoxicity = no statistically significant difference. Nominal = only nominal concentrations reported in publication, No effect = no impacts observed at any concentration tested. For definitions of toxic threshold values and other acronyms see also Table A1, Supplementary materials. For references see end of table.

	Petroleum hydrocarbon	+UVR treatment (μW cm^{-2})	Toxicity, -UVR to +UVR (μg L^{-1})	Toxicity increase
Reef-building corals (Cnidaria)				
Acropora tenuis (L)	Heavy fuel oil (48 h)[1]	A (6 h, 750 day^{-1})	Meta. EC_{50} 96 to 51 (TPAH)	1.9-fold
	Diesel (48 h)[1]	A (6 h, 750 day^{-1})	Meta. EC_{50} 1300 to 494 (TPAH)	2.6-fold
	Gas condensate (24 h)[2]	S (2 h; 4500–6800)	Meta. EC_{50} 339 to 132 (TPAH)	2.6-fold
	Anthracene (48 h)[3]	A (10 h, 680 day^{-1})	Meta. EC_{50} 45 to 6.3	7.1-fold
			LC_{50} 44 to 18.1	2.4-fold
	Phenanthrene (48 h)[3]	A (10 h, 680 day^{-1})	Meta. EC_{50} 91 to 66 (no phototoxicity).	1.4-fold
			LC_{50} >872 (±UVR)	NA
Porites divaricata (A)	Fluoranthene (4.5 h)[4]	S (6 d; NA)	LC_{50} 435.1 to 31.4 (nominal)	13.9-fold
Lobactis scutaria (L) (prev. *Fungia scutaria*)	Pyrene (2 h)[5]	S (1 h; 410–1400)	LC_{100} 48 (nominal; +UVR). Specific -UVR results not reported.	>1-fold
Montipora verrucosa (A)	Pyrene (2 h)[5]	S (8 h; 410–1400)	Bleaching LOEC >48 to 16 (nominal)	3-fold
		A (8 h; 980–1000)	No effect (<48, nominal, ±UVR).	0
Pocillopora damicornis (A)	Pyrene (2 h)[5]	S (8 h; 410–1400)	Bleaching LOEC >48 to 48 (nominal).	>1-fold
		A (8 h; 980–1000)	No effect (<48, nominal, ±UVR).	0
Porites compressa (A)	Pyrene (2 h)[5]	S (8 h; 410–1400)	No effect (<48, nominal, ±UVR).	0
Other cnidarians				
Zoanthus pacificus (A)	Pyrene (2 h)[5]	S (8 h; 407–1428)	No/close to no phototoxicity (<48, nominal).	1
Sponges				
Rhopaloeides odorabile (L)	Gas condensate (24 h)[2]	S (2 h; 4500–6800)	Meta. EC_{50} 16,000 to 13,000 (TPAH).	1.2-fold
Callyspongia diffusa (A)	Pyrene (2 h)[5]	S (8 h; 407–1428)	No effect (<48, nominal, ±UVR).	0
"unidentified black sponge" (L)	Pyrene (2 h)[5]	A (8 h; 975–1000)	LC_{100} >16 (nominal; +UVR).	3-fold
Molluscs				
Ittibittium parcum (A) (prev. *Bittium parcum*)	Pyrene (2 h)[5]	A (8 h; 975–1000)	No effect (<48, nominal, ±UVR).	0
		S (8 h; 407–1428)	No effect (<48, nominal, ±UVR).	0
Lobatus gigas (L)	Fluoranthene (30 min)[4*]	S (NA)	LC_{50} 16 (+UVR, -UVR not reported).	NA
Polychaetes				
Platynereis dumerilii (A)	Pyrene (2 h)[5]	A (8 h; 975–1000)	LOEC >48 to 32 (nominal). 90–100% mortality at 48 (+UVR).	1.5-fold
Crustaceans				
Alpheopsis sp. (L)	Pyrene (2 h)[5]	S (1 h; 407–1428)	LC_{100} >48 to 32 (nominal). Specific -UVR results not reported.	1.5-fold
	Anthracene (2 h)[5]	S (1 h; 407–1428)	LC_{100} >48 to 48 (nominal). Specific -UVR results not reported.	>1-fold
Apolochus likelike (A) (prev. *Amphilocus likelike*)	Pyrene (2 h)[5]	A (8 h; 975–1000)	LOEC >48 to 16 (nominal)	3-fold

[1] Nordborg et al. (2018), [2] Negri et al. (2016), [3] Overmans et al. (2018), [4] Guzmán Martínez et al. (2007), [5] Peachey and Crosby (1995). [4*] Unpublished results as referred to by Guzmán Martínez et al. (2007).

Table 2
Summary of tests investigating the impacts of elevated temperature on petroleum hydrocarbon toxicity towards coral reef organisms detailing experimental parameters and main results. Where multiple endpoints were assessed only results for the most sensitive endpoint were included (for consistency with Australian and New Zealand water quality guidelines as per Warne et al. (2018)). Exposure length and temperature treatments shown in brackets, for further details on pollutants, test methodology and results please refer to Table A3, Supplementary material. Toxic threshold values presented for each temperature, from low to high, where applicable. Measured concentrations reported if available. Toxicity values reported as μg L^{-1} unless otherwise stated. Species & life stage: A = adult, J = juvenile. Petroleum hydrocarbons: B[*a*]P = benzo[*a*]pyrene. Temperature treatment: A = acute exposure. For definitions of toxic threshold values and other acronyms see also Table A1, Supplementary materials. For references see end of table.

	Petroleum hydrocarbon	Temperature treatment	Toxicity, ambient to elevated temperature (μg L^{-1})	Toxicity increase
Reef-building corals (Cnidaria)				
Pocillopora verrucosa (A)	Diesel (84 h)[1]	A (28 & 31 °C)	Dark respiration 0.015 to 0.023 mg O_2 h^{-1} cm^{-2}	1.5-fold
Vertebrates				
Siganus guttatus (J)	Diesel (17 h)[2]	A (28 & 31 °C)	Standard metabolic rate 132 to ~200 mg O_2 kg^{-1} fish h^{-1}	1.5-fold
Opsanus beta (A)	B[*a*]P (24 h)[3]	A (18 & 28 °C)	Uptake rate 0.020–0.031 to 0.051–0.065 μg g^{-1} h^{-1}	1.7 to 3.3-fold

[1] Kegler et al. (2015), [2] Baum et al. (2016), [3] Kennedy et al. (1989).

2.2. Impacts of UVR on oil toxicity (phototoxicity)

2.2.1. Reef-building corals

The co-exposure of corals to UVR increased toxicity of dissolved aromatics in 70% of tests, and the average increase in toxicity was 4.2-fold (15 tests total, Table 1). No phototoxicity was observed in several tests using adult corals where the exposure times of individual PAHs were very short (<8 h). The majority of studies tested the phototoxicity of individual PAHs (Table 1, Fig. 2), but three studies tested complex mixtures on *Acropora tenuis* larvae using light crude (gas condensate) (Negri et al., 2016), diesel (Nordborg et al., 2018) and heavy fuel oil (Nordborg et al., 2018), respectively. The toxicity of the three types of complex aromatic solutions increased by an average of 2.4-fold in the presence of UVR, and impacts were observed at concentrations below what has been observed in the field both following spills (Diercks et al., 2010) and in chronically polluted areas (Baum et al., 2016). Exposure to individual PAHs also led to reduced larval settlement and increased mortality (Overmans et al., 2018; Peachey and Crosby, 1995) with toxicity increases up to 7.1-fold observed in the presence of UVR (Overmans et al., 2018). Mortality and bleaching (loss of symbionts) in adult corals has also been observed at lower concentrations of aromatics or after shorter exposure times in the presence of UVR (Peachey and Crosby, 1995; Guzmán Martínez et al., 2007).

2.2.2. Other invertebrates

Two experimental studies on UVR co-exposure of coral reef invertebrates (including sponges, polychaetes, zoanthids, gastropods and crustaceans) have been published (Table 1). Some additional information is available on other tropical and subtropical organisms, mainly estuarine species and pelagic larval stages of crustaceans (summarised in Table 3). Phototoxic effects on invertebrates were observed in over 80% of experimental tests (across all habitats) with average toxicity increases of 1.7-

Table 3
Average toxicity increases observed for each combination of stressors and taxonomic groupings to date. Average toxicity increases calculated on most sensitive endpoint only for each test, tests where no effect was observed for any stressor combination excluded. Colour indicates extent of published research currently available ranging from no (red) to ≥15 (green). Numbers in parentheses indicate number of tests published to date. Areas of priority for future research are indicated using bold text and borders. Summaries of individual tests and studies for coral reef species available in Tables 1 and 2. Summaries for other tropical and subtropical species reviewed available in Table A2-A4, Supplementary materials. NA = no comparison data available * = only results from one test available. Value presented is the toxicity change observed for the most sensitive endpoint for the only available test. For interpretation of the references to colour in this table legend, the reader is referred to the web version of this article.

	Coral reef species			**All tropical & subtropical species**		
	Oil · UVR	Oil · Temp	Oil · pH	Oil · UVR	Oil · Temp	Oil · pH
Calcareous algae	**(0)**	**(0)**	(0)	(0)	(0)	(0)
Reef-building corals	**4.2-fold (14)**	**1.5-fold* (1)**	(0)	4.2-fold (14)	1.5-fold* (1)	(0)
Sponges	**1.2-fold (3)**	(0)	(0)	1.2-fold (3)	(0)	(0)
Molluscs	**NA (3)**	(0)	(0)	46-fold (9)	(0)	1.5-fold* (2)
Crustaceans	2.3-fold (3)	(0)	(0)	3.4-fold (20)	4.1-fold (5)	1.1-fold (3)
Echinoderms	**(0)**	**(0)**	(0)	12.2-fold (5)	(0)	(0)
Other invertebrates	1.3-fold (2)	(0)	(0)	1.3-fold (2)	(0)	(0)
Fish	**(0)**	**1.5-fold (2)**	(0)	4.6-fold (13)	1.8-fold (6)	>1* (1)
Total	3.2-fold (25)	1.5-fold (3)	(0)	7.2-fold (66)	3.0-fold (12)	1.3-fold (6)
Source:	Table 1 & A2	Table 2 & A3	Table A4	Table A2	Table A3	Table A4

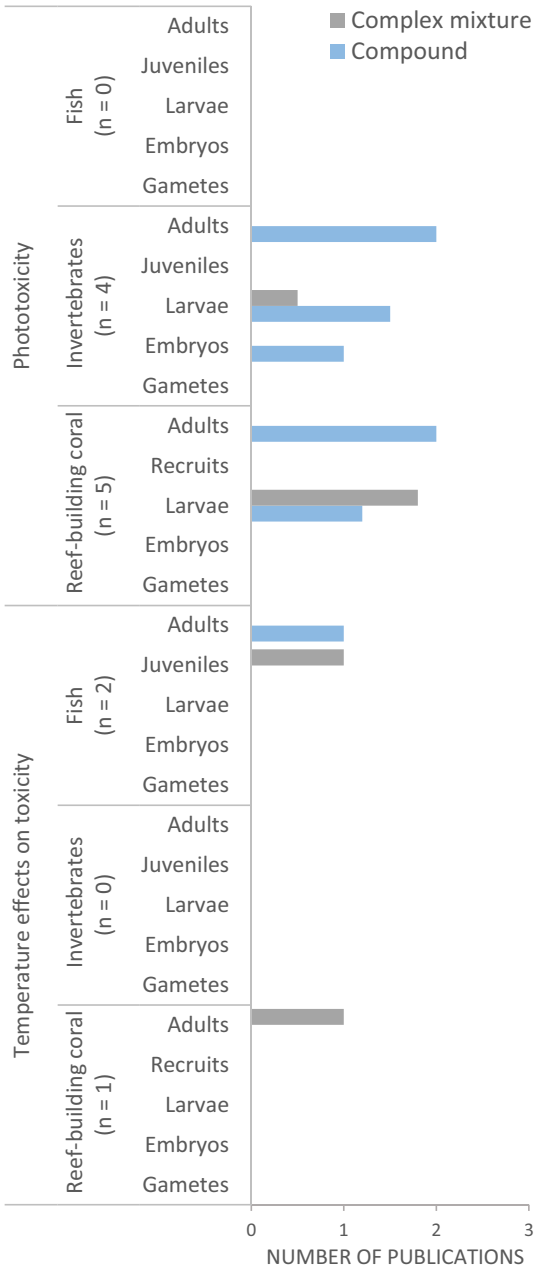

Fig. 2. Number of laboratory studies investigating the phototoxic and temperature effects on petroleum hydrocarbon toxicity towards reef-building corals, non-coral reef invertebrates and fish directly or intermittently associated with coral reefs. Colour indicates the relative proportion of experimental tests performed using individual aromatic compounds or complex mixtures such as oils, respectively. Several publications report on the effects of petroleum hydrocarbons for several taxonomic groups or life stages and may therefore be included in the total number of studies, and bars, for multiple groupings or life stages. n = the total number of publications reporting on tests for each respective grouping. For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.

fold for coral reef invertebrates (9.3-fold across all habitats and tests, Table 3) where petroleum hydrocarbon toxicity was tested in the presence of UVR (Table 1). However, the majority of available information on the impacts of UVR co-exposure on coral reef associated invertebrates originates from a single publication by Peachey and Crosby (1995). Most exposures were acute (Table 1), and therefore tests conducted with adult organisms may underestimate the potential impacts of delayed effects and longer exposures, especially when the often slow uptake and depuration rates observed for 3-ring hydrocarbons is taken into account (Solbakken et al., 1984). Additionally, the UVR intensity and spectrum used in exposures differed between many studies and tests making direct comparisons problematic (see also Section 3.1 of Discussion). In a comparative study, pyrene was generally more toxic than fluoranthene in the presence of UVR and impacts were observed at concentrations as low as 2.7 μg L^{-1} (Peachey, 2005). While a substantial number of tests have been performed, especially using non-reefal tropical and subtropical crustaceans (Table A2), measured PAH concentrations for treatment solutions was reported for <60% of tests. Most of the non-coral invertebrates tested experimentally in the presence of UVR were exposed to individual PAHs (Fig. 2) with survival often being the only endpoint assessed.

2.2.3. Fish

No studies on the interactions between petroleum hydrocarbon toxicity and UVR have been published for tropical coral reef fish. However, studies on the effects of UVR in combination with petroleum hydrocarbons for other tropical and subtropical fish have been conducted using acute tests on fish embryos, larvae and juveniles, i.e. the life stages predicted to be the most sensitive to both individual UVR and petroleum hydrocarbon exposure. All tests showed an increase in toxicity in the presence of UVR for at least one endpoint across habitats, with an average increase of 4.6-fold (Table 3). The observed sensitivity varied with both timing of exposure (e.g. early or late in embryogenesis), exposure length and species. When toxic threshold values are compared across tests, *Seriola lalandi* embryos (Sweet et al., 2018) appear to be more sensitive to exposure than *Sciaenops ocellatus* and *Cynoscion nebulosus* larvae (Alloy et al., 2017), which in turn were more sensitive than *Coryphaena hippurus* embryos exposed prior to hatching (regardless of when exposure took place; Table A2) (Alloy et al., 2016; Sweet et al., 2016).

2.3. Impacts of elevated temperature on oil toxicity

2.3.1. Reef-building corals

The only experimental study on combinations of oil pollution and thermal stress to corals to date reported a 1.5-fold increase in dark respiration of adult *Pocillopora verrucosa* when co-exposed to diesel WAF and elevated temperature (Table 2) (Kegler et al., 2015). Other authors have suggested that synergistic interactions between crude oil and temperature may have caused a growth rate depression in *Pseudodiploria strigosa* (previously *Diploria strigosa*) during laboratory exposures performed at summer temperatures (28 °C) (Dodge et al., 1984). However, more severe behavioural impacts in the same species were observed during exposures performed in winter (18 °C) in a separate study using the same exposure system (Wyers et al., 1986). Additionally, Legore et al. (1989) conducted in situ experiments that indicated coral communities in the Arabian Gulf may be tolerant to brief exposure to oil when water temperatures are favourable, but may be more sensitive at temperatures closer to their thermal limits, or when corals are exposed to additional stressors.

2.3.2. Other invertebrates

No testing of the combined effects of elevated temperature and petroleum hydrocarbons have been performed for reef invertebrates (other than coral) to date. However, tests on non-reefal tropical and subtropical invertebrates suggest that a range of taxa may be more sensitive to oil pollution at high temperatures (Table 3). For example, the toxicity of three oils to grass shrimp (*Palaemonetes pugio*) increased at high temperature treatments (Table A3) (Tatem et al., 1978). The toxicity of Lufeng crude oil WAF also increased with increasing temperature (as well as exposure time and decreasing body size) in a study of 15 species of subtropical copepods across different seasons (Jiang et al., 2012). Elevated temperature (+4 °C above acclimation) has also been reported to reduce the time to lethality for embryos of the same species (Fisher and Foss, 1993). This is consistent with the widely-held notion that uptake of aromatics into cell membranes is accelerated at higher

temperatures (French-McCay, 2002) (Fig. 3). On average, petroleum hydrocarbon toxicity increased 4.1-fold across all tests reviewed in comparison to oil alone at the highest temperatures tested (Table 2 and A3).

2.3.3. Fish

All tests on the combined impacts of elevated temperature and petroleum hydrocarbons on tropical and subtropical fish were acute (≤7 day) exposures during early life stages. Toxicity increased on average 1.8-fold at the highest tested temperature and most studies tested complex aromatic hydrocarbon mixtures (Tables 2–3). Elevated temperature can increase the uptake of PAHs in fish, along with proposed corresponding increases in PAH metabolism and depuration rates (Kennedy et al., 1989) (Table 2; Fig. 3). The standard metabolic rate (SMR) has also been observed to increase at elevated temperature (+3 °C), however, no statistically significant differences could be detected between fish exposed to WAF and control solutions (Baum

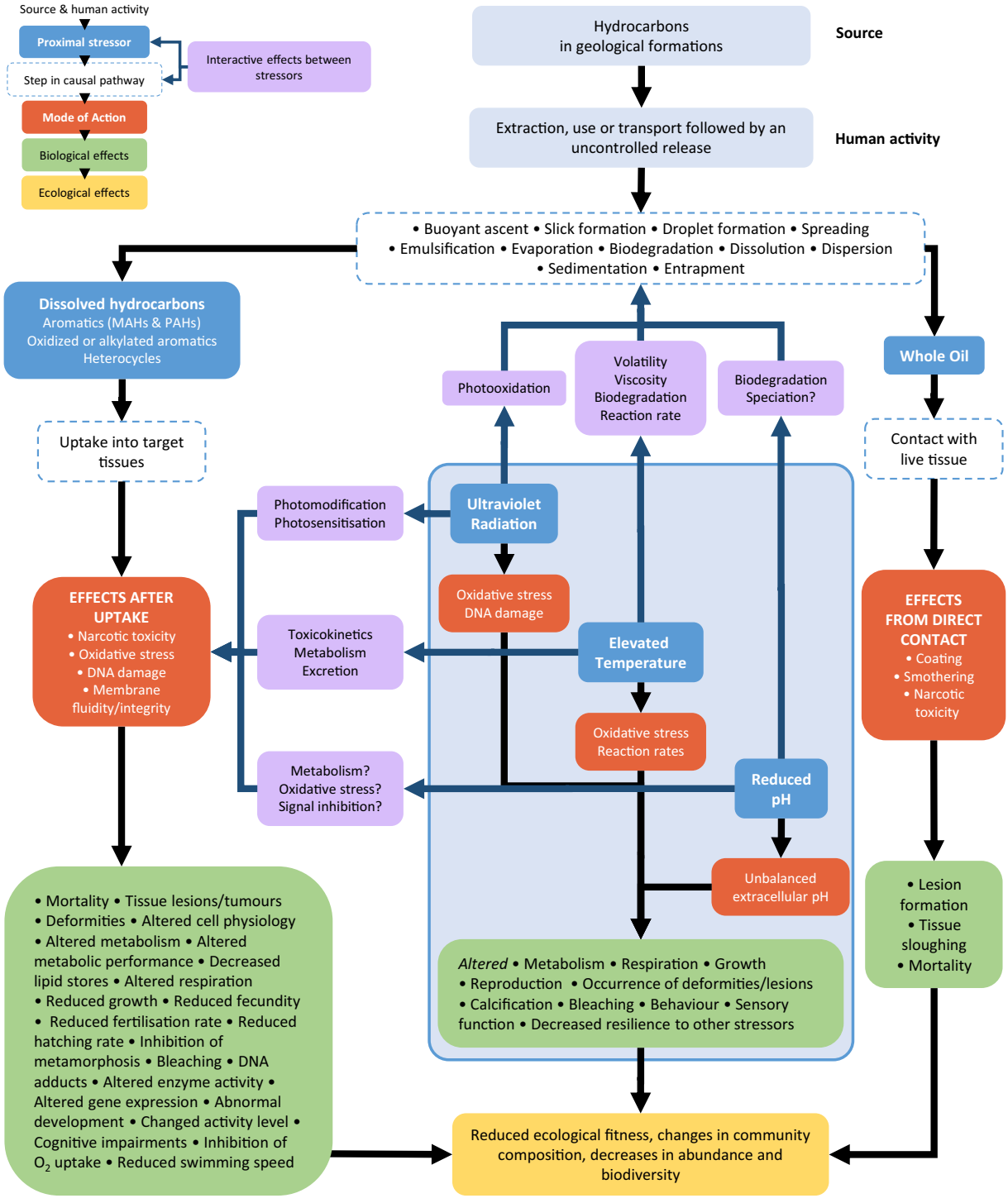

Fig. 3. Conceptual model showing pathway of exposure and summaries of effects from exposure to oil pollutants and tropical environmental pressures (UVR, elevated temperature and reduced pH) on coral reef organisms. Environmental co-factors can affect petroleum oil toxicity towards coral reef organisms (purple boxes) either through direct co-exposure, and resulting interactions, or by affecting oil weathering, dissolution and reaction rates prior to or during uptake into target tissues. For a more detailed conceptual model of oil pollution interaction pathways and effects with UVR, elevated temperature and reduced pH see also Fig. A2, Supplementary materials. For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.

et al., 2016) (Table 2). *Coryphaena hippurus* embryos exposed to oil HEWAF at 30 °C suffered higher mortality rates (anecdotal, no data presented) (Pasparakis et al., 2016; Perrichon et al., 2018) as well as increased impacts on sub-lethal endpoints at lower treatment concentrations than embryos exposed to oil at the control temperature (26 °C) (Pasparakis et al., 2016) (Table A3). In contrast, no increased impact was observed on cardiac functionality in embryos (Perrichon et al., 2018) while juveniles showed no impacts on swim performance from either HEWAF or elevated temperature exposure (Mager et al., 2018). Perrichon et al. (2018) concluded that the PAH exposures affected cardiac functionality more than elevated temperatures, but that elevated temperature may decrease larval resilience to oil exposure by increasing energy demand (Fig. 3).

2.4. Impacts of low pH on oil toxicity

No studies on the interactions between lower than current ambient pH and petroleum hydrocarbons on tropical coral reef species have been published to date.

2.4.1. Non-reefal invertebrates

At low pH, petroleum hydrocarbon toxicity increased 1.3-fold on average for non-reefal invertebrates (Table 3). However, due to a lack of data (only 4 studies across all subtropical-tropical marine environments) it remains unclear whether low pH and oil contamination on marine invertebrates results in additive effects or interactions. In the combinations reviewed here, petroleum hydrocarbons were generally responsible for the majority of negative impacts (Coelho et al., 2015; Asadi and Khoiruddin, 2017; Su et al., 2017; Asadi et al., 2018). However, low pH has been observed to exacerbate toxicity (Table A4). Reported responses to combinations of aromatics and low pH in adult bivalves and larval shrimp include decreased hemocyte counts and phagocytosis (Su et al., 2017), depressed gene expression for pathogen recognition pathways (Su et al., 2017), mortality (Asadi and Khoiruddin, 2017; Asadi et al., 2018), decreased abundance (Coelho et al., 2015) and neurological impacts (decreased activity, loss of balance, comatose states) (Asadi and Khoiruddin, 2017; Asadi et al., 2018) (Fig. 3). However, incomplete reporting of results, exposure concentrations, methods chosen for pH adjustments and statistical analyses means that many of the results are of low reliability.

2.4.2. Fish

In the single study testing the effects of oil pollution and low pH on a marine fish with a tropical to subtropical distribution, Sun et al. (2018) found no influence of high pCO_2 (low pH) on the sensitivity of *Oryzias melastigma* to oil WAF (Table 3 and A4). However, co-exposure with low pH increased impacts on some sub-lethal endpoints in comparison to individual stressor exposures (Sun et al., 2018) (Table A4; Fig. 3). Overall, early life stages were more sensitive to low pH than oil exposure but most sensitive to the combined effects of both stressors (Sun et al., 2018).

3. Discussion and synthesis

The tests reviewed show that UVR and elevated temperature exposures increased the toxicity of petroleum hydrocarbons to coral reef organisms on average 3.2-fold and 1.5-fold, respectively, with no reliable information currently available on the effects of low pH on oil toxicity (Table 3). When expanded to include species across all tropical and subtropical habitats that may intermittently occur near coral reefs, the average increases in toxicity was 7.2-fold, 3.0-fold and 1.3-fold when co-exposed to UVR, high temperature and low pH, respectively. These numbers should be considered with caution, due to the limited data, lack of study replication, the often incomplete experimental descriptions (e.g. no chemical analysis) and low taxonomic coverage. Nevertheless, it is evident that studies which do not incorporate environmental conditions relevant to shallow tropical reef environments will, on average, underestimate the potential impacts of oil pollution towards coral reef organisms.

The following sections further evaluate the evidence for UVR, high temperature and low pH influence on the toxicity of dissolved aromatics from petroleum on tropical species and identify knowledge gaps and approaches to improve the environmental relevance of experimentally-derived toxicity thresholds for this ecosystem of high ecological value.

3.1. Impacts of UVR on oil toxicity

Phototoxicity is almost certain to occur for any oil spill affecting oligotrophic shallow coral reef environments during the day (Barron et al., 2009; Michael et al., 2012; Bridges et al., 2018; Overmans and Agustí, 2019), and UVR exposure needs to be considered in all studies that aim to derive toxicity thresholds for risk- or natural resource damage assessments for coral reef environments.

3.1.1. Quantifying the effects of phototoxicity

The observed increase in oil toxicity when co-exposed to UVR varied for different compounds, complex mixtures, UVR sources, UVR intensities and study species. UVR increased the toxicity of both individual aromatics and complex mixtures towards tropical and subtropical organisms of all taxonomic groupings reviewed here. The observed phototoxicity varied between both compounds and tests for the individual aromatics (1.3-fold to 87-fold increases), while the toxicity increased 4.3-fold on average for complex mixtures, with increases up to 9.3-fold observed (Stieglitz et al., 2016). This wide variation in phototoxicity is due in large part to the unique phototoxic potential of each PAH, as determined by physical and chemical parameters such as ring conjugation (Mekenyan et al., 1994; Veith et al., 1995). The increase in toxicity generally occurs after uptake and accumulation of PAHs in the organism's tissues (Arfsten et al., 1996), with photosensitisation (generally oxidative damage to DNA, lipids and membrane proteins due to ROS (Viswanathan and Krishna Murti, 1989; Arfsten et al., 1996; Barron, 2017); Fig. 3) considered the primary mechanism. These effects (oxidative stress and direct DNA damage) have been observed in coral reef organisms following exposure to UVR (Banaszak and Lesser, 2009) and petroleum hydrocarbons individually (Fig. 3), with follow on impacts on competitiveness (Gleason and Wellington, 1993; Kuffner, 2001; Banaszak and Lesser, 2009; Dobretsov et al., 2010), survival (Banaszak and Lesser, 2009; Lamare et al., 2011), settlement success of larvae (Kuffner, 2001; Dobretsov et al., 2010) and resilience to other environmental pressures (Banaszak et al., 2003; Yee et al., 2008) also reported (Fig. 3). The toxicity increased with UVR co-exposure for the majority of tests across the taxonomic groups reviewed here, providing some confidence in the overall trend. However, given the lack of replication of tests and often poor characterisation of UVR intensity and spectra, further work is needed to clarify the scale of influence of UVR on toxicity. In the meantime, the conservative approach in the context of risk assessments and management would be to account for observed phototoxicity until additional data becomes available.

The variability in phototoxicity between individual compounds can be predicted using the quantitative structure-activity relationship for each compound (Mekenyan et al., 1994) (see Section 3.3). However, these predictions may not always be transferable across different taxa or compounds, and largely depend on the experimental conditions. For example, pyrene is expected to be one of the most phototoxic aromatics (Mekenyan et al., 1994); however, fluoranthene showed a higher average toxicity increase (22-fold) than pyrene (2.9-fold) across the tests reviewed here. One explanation for this apparent discrepancy could be the difference in wavelengths at which UVR is absorbed between these PAHs. The absorbance maximum for pyrene lies in the UVB range (Mekenyan et al., 1994), while fluoranthene has absorbance maxima in both the UVA and UVB spectrum. It follows that any tests that exclude UVB may underestimate phototoxicity, highlighting the

critical requirement to apply an environmentally relevant spectrum and intensity of UVR and visible light, and to accurately characterize it in oil toxicity tests (Nordborg et al., 2018).

The additional hazard posed by UVR co-exposure also depends on the composition of the oil, the UVR intensity, the sensitivity of individual species and life stages and the exposure to both stressors (Barron, 2017). There are at least three ways that this can be addressed: (i) by further experimental toxicity testing with UVR and oil (including repeating experiments where possible to assess response variability within species or populations); (ii) by modelling phototoxicity based on structure-activity relationships (Section 3.3) and (iii) by field observations following spills (Section 3.4). These approaches are complementary and all need to be undertaken to improve how phototoxicity is accounted for in risk assessments.

In the absence of comprehensive experimental data, application of safety factors to current threshold values or guidelines to account for phototoxicity can be employed. The 10-fold adjustment to toxicity thresholds suggested by French-McCay et al. (2018) to account for phototoxicity in waters <20 m depth in the Gulf of Mexico, appears to be sufficiently conservative to account for an average toxicity increase in the presence of UVR for the reviewed tropical and subtropical marine organisms (Table 3). However, greater toxicity increases have been observed for some marine invertebrates (Spehar et al., 1999; Guzmán Martínez et al., 2007), and some of the current literature may underestimate phototoxicity due to the UVR sources used in the toxicity testing. While the application of an UVR-adjustment is useful as an interim measure in coral reef management, further toxicity testing of keystone reef species is required to validate the scale of this adjustment.

3.1.2. Improving and prioritising experimental testing for phototoxicity to tropical reef species

The need for standardisation of oil toxicity testing has long been recognised, including the quantitative analysis of treatment solutions (Singer et al., 2000; Aurand and Coelho, 2005; Coelho et al., 2013; Redman and Parkerton, 2015). These principles regarding solution preparation, experimental methodology and analysis also apply for oil toxicity testing which includes additional co-factors such as UVR. In the oil phototoxicity tests reviewed here only 36% measured and reported the chemical composition of tested solutions (prior and post exposure). To ensure that the data produced is comparable and applicable, chemical analysis of treatment solutions should be performed, at a minimum, for each level of the co-factor investigated e.g. both in the presence or absence of UVR or at each UVR exposure intensity (e.g. 0, 10, 50 or 100% UVR shading) or spectrum. Furthermore, a wide variety of exposure methods remain in use for both single and multi-factorial testing of oil toxicity (including static, static-renewal, flow-through, open and closed systems), likely contributing to the variability in sensitivity observed. Not adhering to standard experimental protocols remains an issue across all oil toxicity research and efforts should be made to ensure exposure types and systems used are comparable.

3.1.2.1. Prioritising species and life stages. Organisms most likely to be co-exposed to high levels of UVR during an oil spill include: shallow reef-building algae and corals, soft corals, anemones, sponges and clams as well as territorial (e.g. shrimps, damsel fish and anemone fish) or slow moving (e.g. sea urchins, feather stars and gastropods) organisms found <10 m from the surface. Reef-building corals were the most studied coral reef taxa reviewed, but most of the 14 tests were conducted using different hydrocarbons, exposure systems and UVR exposures, making direct comparisons of sensitivity impractical. Along with reef-building corals, algae and sensitive invertebrates (e.g. bivalves and echinoderms; Table 3), additional testing of representative crustaceans and reef fish should be performed as their sensitivity to the narcotic effects of petroleum hydrocarbons can be high and no comparative testing has been performed in the presence of UVR (Table 3). Representative species of functionally important taxa that commonly occur in shallow, UVR-exposed areas of the reef should be prioritised, especially species with wide geographical ranges. Due to the extent of the knowledge gap it is recommended that experimental efforts primarily focus on life stages of representative species likely to be most sensitive to exposure (e.g. embryos, larvae and life stage transitions from larval to adult forms), and on taxa which contribute to maintaining reef structure (corals, calcareous algae), followed by the least investigated and most sensitive phyla (sponges, echinoderms, fish; Table 3). No tests of oil toxicity have been performed on gametes/fertilisation in the presence of UVR, and this should be addressed, as some broadcast spawning species of corals (Plathong et al., 2006; Bronstein and Loya, 2011; Suzuki, 2012) and fish (Craig, 1998; Sancho et al., 2000) release gametes during the day. Of particular note are calcareous algae and echinoderms where large scale in situ impacts (e.g. 80% mortality) have been observed following spill events on or near coral reefs (Ballou et al., 1989; Jackson et al., 1989; Green et al., 1997), but no laboratory studies have been performed to assess phototoxicity (Table 3). Impacts on these taxa could also have downstream effects on coral reef communities due to their importance as a cue for coral larval settlement (Heyward and Negri, 1999) and herbivory (Sammarco, 1982).

3.1.2.2. Standardising hydrocarbons for phototoxicity testing. The choice of ecologically important species that represent coral reefs broadly should be complemented by testing oil types that are commonly extracted, transported or used near coral reefs. A clear obstacle for comparing phototoxicity for tropical species in this review was that 17 different oil types and individual compounds were applied in the 66 tests (along with multiple solution preparation and exposure methods). As every oil type has a different general toxicity and phototoxic potential (Redman and Parkerton, 2015; Forth et al., 2017), standardising the oil types to a limited number of specific heavy fuel oils, diesels, light or heavy crudes would facilitate between-species comparisons in future studies and improve estimates of phototoxicity for coral reef species. The selection of a few common pure aromatics for phototoxicity testing is also important as this allows direct comparisons in phototoxicity of identical compounds between studies and can contribute data to improve phototoxicity modelling (see Section 3.3). The chemical analysis and reporting of expected photooxidation products in tested solutions would also improve our understanding of the phototoxic pathways (Pelletier et al., 2006).

3.1.2.3. UVR intensity and spectral quality. Standardising the UVR intensity and spectral quality applied in phototoxicity experiments is also crucial to maximise the ability to compare phototoxicity between studies on coral reef species. Phototoxicity of petroleum hydrocarbons was reported across tropical and subtropical taxa in response to both ambient solar UVR and UVR from artificial sources in tests reviewed here. The inclusion of UVR in light spectra used for experimental work on coral reef taxa is currently rare, both in oil ecotoxicological work and coral reef research as a whole, unless outdoor systems are used. Solar UVR has the advantage of providing the most ecologically relevant spectrum when experiments are performed close to the origin of the study organisms (Negri et al., 2016; Alloy et al., 2017). However, both daily and seasonal variability in solar radiation intensity reduces the comparability of studies both between different geographical regions and between test days (see e.g. Tedetti and Sempere (2006) and Alloy et al. (2017)). UVR exposures (spectrum and intensity) similar to natural UVR conditions on coral reefs can be generated artificially (Nordborg et al., 2018) (Fig. 4), and have the advantage of being comparable across studies if materials and experimental systems are adequately described. Additionally, some studies have shown that artificial UVR can produce similar phototoxic responses as ambient solar UVR in individual PAHs (Spehar et al., 1999) and oils (Nordborg et al., unpublished data). For comparison among studies and quantification of phototoxicity the attenuation by exposure chambers used needs to be measured and the full spectral characterisation and intensity of exposures reported,

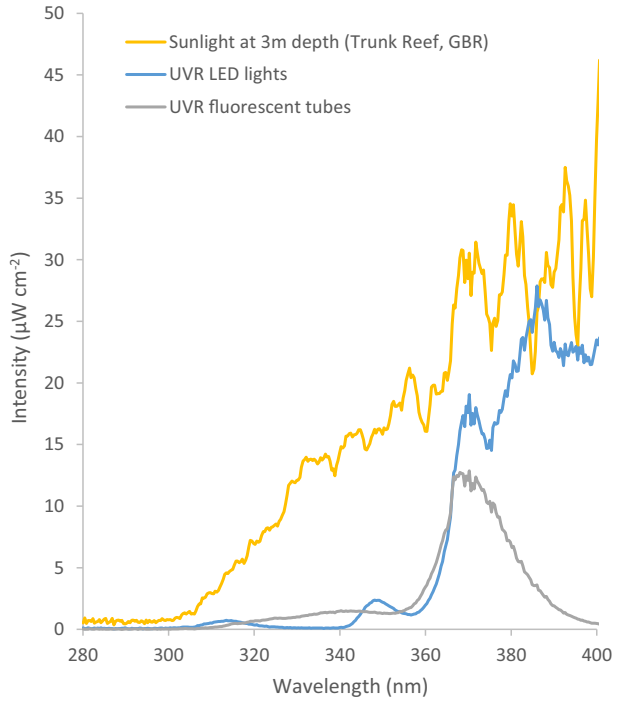

Fig. 4. Comparison of spectrum of artificially generated ultraviolet radiation (UVR) to that observed at 3 m depth on Trunk reef, central Great Barrier Reef (Australia). Artificial UVR spectrum generated from LED panel lights developed in the National Sea Simulator, Australian Institute of Marine Science, Queensland Australia (blue line), and from fluorescent tubes used by Nordborg et al. (2018) (grey line) compared to spectrum observed at 3 m depth at Trunk Reef (central Great Barrier Reef, Australia) in spring (yellow line; adapted from Nordborg et al. (2018)). For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.

preferably in relation to a reference value for the natural habitat of the tested species or population.

3.1.2.4. Exposure sequence and phototoxicity. The exposure method or sequence used in oil toxicity testing can substantially affect phototoxicity. While phototoxicity is primarily considered to result from photosensitisation (Viswanathan and Krishna Murti, 1989; Arfsten et al., 1996; Barron, 2017), this mechanism does not always account for all of the observed phototoxic effects (Choi and Oris, 2000). Photomodification, the production of toxic (commonly oxidized) intermediates from parent PAHs, or other compounds (Viswanathan and Krishna Murti, 1989; McConkey et al., 2002; Lee, 2003) (Fig. 3), can also contribute towards (or sometimes reduce) the total phototoxicity observed for oils and oil compounds (Barron, 2017). Approximately 50% of the tests reviewed here used co-exposure to UVR and petroleum hydrocarbons with the remaining tests applying sequential exposures or not clearly stating how exposures were performed (see also Table A2 for further details). The most common form of sequential exposure in reviewed tests was to expose organisms to the pollutant first followed by UVR exposure in uncontaminated seawater, targeting photosensitisation. However, oil spills in coral reef environments are likely to also result in pre-exposure of pollutants to UVR, which allows for photomodification to occur in both the slick as the slick weathers (also termed oil photooxidation) or in dissolved fractions (Fig. 3). Indeed, partial photooxidation of slick oil was recently shown to have constituted a major fate of surface oil during the Deepwater Horizon spill (Ward et al., 2018) and photooxidation increases the water solubility of both aliphatic and aromatic petroleum compounds (King et al., 2011; Ray et al., 2014; Ward et al., 2018). In tests reviewed here the type and amount of oil weathering affected the phototoxicity observed. Irradiation of floating oil, oil WAF and dissolved individual PAHs has been shown to increase both the abundance of oxygenated compounds (responsible for toxicity increases through the photomodification pathway) in the aqueous fraction (Ray et al., 2014) (Fig. 3) and observed toxicity (Pelletier et al., 2006). Despite this likely scenario, pre-exposure of petroleum oil contaminants to UVR have so far not been conducted for any coral reef associated taxa. Comparative studies using both types of sequential exposure in representative coral reef species would clarify the relative contributions of photomodification and photosensitisation to the total phototoxicity in coral reef environments. However, the use of data from sequential exposures may underestimate the impacts of petroleum hydrocarbon mixtures by excluding the contributions from one of the two pathways. Therefore, co-exposure to petroleum hydrocarbons and UVR is suggested as the preferred method for testing the combined effects of narcotic toxicity and phototoxicity of petroleum hydrocarbons and for generating toxicity threshold data for use in risk assessments and management.

3.2. Impacts of elevated temperature and low pH on oil toxicity

3.2.1. Accounting for thermal anomalies

Many tropical species live close to their upper thermal limits (Hoegh-Guldberg, 1999; Rummer et al., 2014; Habary et al., 2016), and elevated temperature has been identified as a key co-factor that reinforces the negative impacts of other stressors in >50% of literature on multiple and cumulative impacts affecting coral reef species (Ban et al., 2014). This review found that elevated temperature generally increased the effects of petroleum exposure in corals, non-coral invertebrates and fish, with increased uptake rates also reported. The number of studies and tests was low (Table 3) and the experimental designs applied prevented a quantitative assessment of the interaction between the two pressures. However, elevated temperature increased impacts for at least one endpoint in >80% of studies (across habitats), and toxicity increases of up to 12.6-fold at high temperatures were reported.

Temperature affects the rate of biochemical functions in ectothermic organisms and this has follow-on effects at cellular, organism and community levels (Nguyen et al., 2011). Impacts of elevated temperature alone broadly include increased oxidative stress in phototrophs (Przeslawski et al., 2008; Mydlarz et al., 2010), bleaching (loss of coral symbionts) and associated decreases in fecundity, growth rate and mortality (Mydlarz et al., 2010), impacts on reproductive success and timing (Przeslawski et al., 2008; Donelson et al., 2010), aerobic scope (Rummer et al., 2014), behaviour (Biro et al., 2010) and survival (Rummer et al., 2014) as well as increased activity and reduced growth rates (Przeslawski et al., 2008) (Fig. 3). Increases in pollutant toxicity due to elevated temperatures generally results from increased rates of uptake, chemical reactions and metabolism (Korn et al., 1979; Viswanathan and Krishna Murti, 1989; French-McCay, 2002) (Fig. 3), but the change in toxicity is species- and compound-specific (Korn et al., 1979). The impacts of temperature on reaction rates (chemical and biological), the solubility of aromatic compounds in water and lipids (Korn et al., 1979; Saeed et al., 1998; French-McCay, 2002) (Fig. 3) and the increased toxicity observed in the studies reviewed here indicate that the impacts of oil pollution may generally be more severe (or at least rapid) at elevated temperatures. At high temperatures the time to reach maximum accumulation of aromatics in lipid membranes is generally reduced (French-McCay, 2002), which may be particularly important for short to moderate exposure periods. In addition, the volatility of MAHs and low molecular weight PAHs, as well as the reaction rates associated with the chemical and bio-degradation of aromatics, may increase in tropical conditions compared to in cooler climates (increased rate of weathering; Fig. 3). This may influence the exposure period to toxic components and the composition of the resulting mixture (Neff et al., 2000; French-McCay, 2002; Jernelöv, 2010), further confounding the response of tropical species to hydrocarbon pollution even at current summer temperatures in the tropics.

There is little consensus on the comparative sensitivity to pollutants of organisms from different climates (e.g. tropical and temperate). Statistical comparisons of threshold values and sensitivities of individual species have indicated that some tropical fish were not more sensitive than fish from other climates, however no aromatic compounds were compared (Dyer et al., 1997). Another comparison concluded that oil thresholds derived for non-Arctic species would be protective of Arctic species (Bejarano et al., 2017). The dataset also included four tropical species, too few to draw any conclusions as to whether tropical species are inherently more or less sensitive than temperate or polar species under ambient temperature regimes. The relationship between narcotic toxicity of oil and temperature can be accounted for in toxicity modelling (French-McCay, 2002; McGrath and Di Toro, 2009), but so far this has not been empirically validated for tropical reef species at maximum summer temperatures or under heatwave conditions (e.g. 1–2 °C above average maximum summer temperatures).

While the available data indicates elevated temperatures increase the toxicity of petroleum hydrocarbons to tropical species, more controlled multi-factorial studies are needed to understand the quantitative relationships between these stressors to predict the scale of influence that heating events may have on the hazards posed by oil pollution to coral reef species. Testing the temperature dependency of oil toxicity towards key species across multiple taxonomic groupings is recommended to facilitate the validation and use of predictive toxicity models at tropical temperatures. As suggested for UVR co-exposure, the initial focus should be on habitat forming reef species such as corals and coralline algae, followed by potentially sensitive invertebrates and fish. To effectively quantify the influence of elevated temperature on oil toxicity, studies would need to acclimate organisms at average summer temperatures and include several elevated temperatures, including those reached during current heatwaves and those projected over the coming century. As discussed for phototoxicity studies, quantitative chemical analysis of treatment solutions should be performed for each temperature treatment level tested. Since there is a high likelihood of co-exposure to UVR to shallow coral reef organisms, this additional co-factor should be routinely applied in studies that investigate the impact of high temperatures on oil toxicity thresholds for risk assessments.

3.2.2. Accounting for ocean acidification

Ocean acidification (the lowering of oceanic pH (Hoegh-Guldberg et al., 2007)) represents an additional long-term stressor to consider in relation to petroleum hydrocarbon toxicity; however, the impacts of low pH on petroleum hydrocarbon toxicity remain unstudied for coral reef species (Fig. 3 and Table 3). In the four studies of non-reefal species reviewed here, a trend of increasing toxicity with decreasing pH was observed (1.3-fold; Table 3), indicating that both low pH observed during diel pH cycles (Price et al., 2012) and future pH conditions may exacerbate the negative impacts of petroleum hydrocarbons in both fish and invertebrates. While there is very limited information on how low pH influences oil toxicity, it can interact with thermal stress to reduce both coral and crustose coralline algae health (Anthony et al., 2008; Pandolfi et al., 2011), potentially making important reef-builders more vulnerable to local stressors. OA could also exacerbate the effect of pollutants such as oils by also affecting respiration and photosynthesis rates (Nikinmaa, 2013; Zeng et al., 2015) (Fig. 3). When an additional relevant factor such as UVR is considered, the response can be less predictable. Low pH can exacerbate the damaging effects of UVR by compromising calcified tissues (Häder et al., 2011), increasing the toxicity of heavy metals (Roberts et al., 2013) and affecting the fate (including speciation and bioavailability) of some pollutants (Nikinmaa, 2013; Zeng et al., 2015) (Fig. 3). The effects can also be counterintuitive, with UVR shown to mitigate the negative effects of low pH in a temperate floating oil mesocosm study (Coelho et al., 2015). Multiple factors can also interact independently of the biota. For example, the intensity of potentially harmful UVR may increase if particulate organic material and coloured dissolved organic material in the water column above reefs are reduced due to OA as predicted under some climate scenarios (Banaszak and Lesser, 2009). Additionally, low pH can affect the degradation of spilled oils through changes to microbial community composition (Coelho et al., 2015) (Fig. 3), or reducing the bioavailability of metal co-factors, oxygen and nutrients required for oil degradation (Zeng et al., 2015), indirectly prolonging exposure and the window for interactions with other environmental pressures. As for investigations on the impacts of UVR and elevated temperature on oil toxicity the initial focus of future research should be on taxa which are likely to be sensitive to co-exposure to oil and low pH, in particular reef-builders such as coral and crustose coralline algae. All considerations regarding experimental methodology, chemical analysis and quantification of co-factors discussed in relation to UVR and elevated temperature should also be considered in the context of low pH. However, while the potential impacts of low pH on oil toxicity should also be investigated, UVR co-exposure is more likely to coincide with a spill event and to have a greater influence on the consequences of oil pollution events. Therefore it is recommended that investigations of UVR co-exposure be prioritised over low pH.

3.3. Advancing toxicity modelling for tropical reef species

Additional standardised experimental studies are required to quantify phototoxicity and the influence of high temperatures on oil toxicity to coral reef species; however, oil toxicity modelling that accounts for the effects of these co-factors offers a complementary approach that could be applied to all spill types and scenarios. Predictive modelling of the general (narcotic) toxicity of oil spills in marine environments has been available for over two decades (French-McCay, 2002; Redman et al., 2012); however, the lack of toxicity data for tropical marine species means that it is unclear whether toxic thresholds derived from predictive oil toxicity models based on tests of taxa or species from cooler climates are protective of coral reef organisms in warm waters. Currently the databases for neither of the main predictive (narcotic) toxicity models used (PetroTox (Redman et al., 2012; Redman et al., 2017) and OilToxEx (French-McCay, 2002)) include coral reef species. Predictive toxicity modelling for oil spills therefore needs to be extended to include, and be validated for, coral reef species under relevant ambient tropical, and heatwave, temperature conditions. Toxicity models that account for heatwaves could be progressed by performing toxicity tests with a selection of pure aromatics under standard experimental conditions as well as at mean summer maximum temperatures and conditions relevant to heatwaves. More recently, a toxicity model that calculates oil phototoxicity has been developed (Marzooghi et al., 2018). The phototoxic target lipid model (PTLM) takes the light spectrum, intensity at each wavelength and exposure duration into account, and has been validated for acute toxicity predictions for both individual aromatics and mixtures (Marzooghi et al., 2016; Marzooghi et al., 2018) towards some aquatic species. So far, only two marine tropical (non-reefal) species have been used in validation of predictions for individual compounds (Marzooghi et al., 2016), while none were used for validation of mixtures (Marzooghi et al., 2018). Additionally, the likely contributions of methyl-substituted aromatics to phototoxicity (Finch et al., 2017) are yet to be incorporated in the models. Calculating phototoxicity using the PTLM represents a promising tool for improving the application of toxicity models to predict toxic thresholds for oil spills to coral reef species and should be validated against key coral reef species and life stages prior to application in coral reef management or risk assessments.

3.4. Improving field studies to interpret oil-multiple stressor interactions

There have been many studies monitoring the ecological damage to shallow coral reefs following oil spills (Rinkevich and Loya, 1977; Loya and Rinkevich, 1980; Bak, 1987; Ballou et al., 1989; Burns and Knap, 1989; Jackson et al., 1989; Garrity and Levings, 1990; Guzmán et al., 1991; Guzmán et al., 1994; Krupp and Abuzinada, 2008; Renegar et al., 2017). However, in most cases information on the environmental

conditions (including temperature, light spectrum, UVR intensity and pH) or dissolved aromatic concentrations during the spill are lacking. Therefore, differences in impacts that have been observed (e.g. greater toxicity in shallow water (Bak, 1987; Burns and Knap, 1989; Jackson et al., 1989; Green et al., 1997) or proximity to source (Smith et al., 1987; Green et al., 1997)) cannot readily be attributed to any specific factor or gradient thereof. It is likely that one or several environmental factors could be affecting the ecological impact of each spill event, especially when considering the high likelihood of high UVR exposure and possible thermal stress at the spill sites (see e.g. Sheppard (2009), Price et al. (2012) and Nordborg et al. (2018)), and their potential influence on oil toxicity. It has been recommended that future monitoring and impact assessments of oil spills in coral reef environments include measurements of temperature, salinity, dissolved oxygen, turbidity and chlorophyll addition to dissolved hydrocarbon sampling along gradients of increasing depth and distance from the spill source (Hook et al., 2016). In addition to these, monitoring of UVR spectra and intensity as well as pH are recommended based on the findings of this review. This more comprehensive sampling regime would help determine the main drivers of impacts during oil spill events, clarify some of the currently unexplored potential interactions between oil toxicity and the reviewed environmental factors (Fig. 3) and inform oil spill risk assessments (e.g. when and how to account for UVR and thermal stress in risk models). An improved understanding of the in situ conditions in reef habitats during spill events, including spatial and temporal gradients of each stressor, would also assist in the design of more ecologically relevant multi-stressor toxicity tests.

4. Conclusions

Co-exposure to UVR, elevated temperature and low pH can increase the toxicity of petroleum hydrocarbons to tropical marine species. Of these environmental co-factors, UVR causes the largest average toxicity increases, highlighting the importance of considering UVR exposure when assessing the risks associated with oil spills. Since it is prevalent in oligotrophic shallow-water coral reef environments it is essential that UVR is explicitly addressed in coral reef oil toxicity studies. Co-exposure, as opposed to sequential-exposure treatments, is recommended. While the use of artificial UVR sources is recommended to ensure comparability and reproducibility, natural sources may also be used as long as the full spectral characterisation and intensity of exposures are adequately described and justified. Additionally, the need for chemical analysis at each exposure level of any co-factor investigated in oil toxicity studies is emphasised. Changes in sea surface temperature and OA already constitute a threat to coral reefs (Hoegh-Guldberg et al., 2017; Hughes et al., 2017), and the most important driver of coral reef habitat loss is the increase in frequency and severity of summer heating events (Hughes et al., 2018). Notably, there are very few studies on the effects of thermal stress on coral reef oil ecotoxicology and further investigations are necessary to assess how the risks posed by oil spills to coral reefs may change during summer heatwave events, both now and as the climate continues to change. Until predictive toxicity modelling can account for UVR and summer temperatures relevant to the tropics, toxicity thresholds calculated from toxicity modelling should be adjusted as outlined by French-McCay et al. (2018) or according to new empirical data relevant to tropical species and conditions (building upon Table 3). The application of projected future temperature and pH conditions in toxicity tests under relevant UVR exposure will be essential for providing policy makers and managers relevant information on the effects of pollutants, including petroleum hydrocarbons, under climate conditions predicted for the upcoming century.

Author contributions

MN and AN planned the review with input from RJ and MO. MN performed the literature search, data collection and review with input from AN, RJ and MO. The manuscript was written by MN and AN with additional input from RJ and MO. Figures and tables created by MN with input from AN, RJ and MO. All authors reviewed and edited the complete manuscript.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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