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Ecological vulnerability of the chondrichthyan fauna of southern Australia to the stressors of climate change, fishing and other anthropogenic hazards

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Abstract

We develop a potentially widely applicable framework for analysing the vulnerability, resilience risk and exposure of chondrichthyan species to all types of anthropogenic stressors in the marine environment. The approach combines the three components of widely applied vulnerability analysis (exposure, sensitivity and adaptability) (ESA) with three components (exposure, susceptibility and productivity) (ESP) of our adaptation of productivity–susceptibility analysis (PSA). We apply our 12-step ESA–ESP analysis to evaluate the vulnerability (risk of a marked reduction of the population) of each of 132 chondrichthyan species in the Exclusive Economic Zone of southern Australia. The vulnerability relates to a species' resilience to a spatial (or suitability) reduction of its habitats from exposure to up to eight climate change stressors. Vulnerability also relates to anthropogenic mortality added to natural mortality from exposure to the stressors of five types of fishing and seven other types of anthropogenic hazards. We use biological attributes as risk factors to evaluate risk related to resilience at the species or higher taxonomic level. We evaluate each species' exposure to anthropogenic stressors by assigning it to one of six ecological groups based on its lifestyle (demersal versus pelagic) and habitat, defined by bathymetric range and substrates. We evaluate vulnerability for 11 scenarios: 2000–2006 when fishing effort peaked; 2018 following a decade of fisheries management reforms; low, medium and high standard future carbon dioxide equivalent emissions scenarios; and their six possible climate–fishing combinations. Our results demonstrate the value of refugia from fishing and how climate change exacerbates the risks from fishing.

KEYWORDS

adaptive capacity, ecological risk assessment, ecological sensitivity, productivity and susceptibility analysis, resilience, stress exposure

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1 | INTRODUCTION

Fishery harvest and by-catch rates for much of the chondrichthyan fauna (sharks, rays and chimaeras) worldwide have been too high over the past half-century (FAO, 2000; Stevens et al., 2000; Walker, 1998). For most of more than 1,250 extant chondrichthyan species globally (Dulvy et al., 2017), there are insufficient data to allow adequate assessment of their conservation status. For example, a summary of 1,041 chondrichthyan species assessed for their extinction risk status according to *The IUCN Red List of Threatened Species* categorizes 17.4% as threatened, 34.0% as near threatened or least concern and 48.6% as data deficient (Dulvy et al., 2014). The poor conservation status and limited information for many of these species, together with mounting ecological changes from climate change and other growing anthropogenic hazards (e.g., inshore construction and chemical contamination) in the marine environment, create an urgent need to find new and comprehensive approaches to prioritizing species for immediate mitigation, monitoring and research.

The susceptibility of chondrichthyans to capture by a wide range of fishing methods and their characteristically low population productivity have resulted in stock declines to low levels for many of these species. Concern over unsustainable catches of these species, together with the potential loss of biodiversity and changes to the structure and function of marine ecosystems, provoked the development of the *International Plan of Action for the Conservation and Management of Sharks* through the Food and Agriculture Organization of the United Nations (FAO, 2000). This plan broadens the term 'sharks' to include all chondrichthyan species.

Improved understanding of the impacts of all anthropogenic hazards on the world's chondrichthyan fauna requires complex integrated models of the climate, oceanography, ecosystems and population dynamics of individual species using large long-term monitoring data sets. Given the present limitations of such models and the lack of suitable data sets, we combine, adapt and extend various rapid assessment methods to provide a framework for comparing risks among species. Distinguishing subjective from objective and relative from absolute elements of risk is inevitably uncertain. Nevertheless, explicit rules for assigning risk provide a transparent and repeatable method for ranking the species. We develop rules based mainly on equations for determining risk at the level of individual biological or ecological attributes (traits) that contribute to a species' inherent resilience to anthropogenic and natural ecological stressors.

We treat these attributes individually, or in combination, as risk factors and combine them in various ways to determine the overall inherent resilience expressed as risk (hereafter referred to as 'resilience risk') and the 'vulnerability' of species to anthropogenic stressors. We distinguish between resilience risk and vulnerability to one or more stressors, such that vulnerability is the risk when exposed to stressors, and 'resilience risk' is the inherent risk to those stressors in the absence of exposure to them.

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Our approach to vulnerability analysis, designed to account for chondrichthyan species' biological characteristics, can be readily adapted for assessing risks to chondrichthyan species in any region of the world. Our approach also applies to other taxa, but it may require adapting some of the equations we use to calculate risk. Most risk assessments aim to determine risk for a wide range of marine aquatic taxa within one framework. However, treating chondrichthyan taxa (*K*-selected) separately from teleost and invertebrate taxa (typically *r*-selected) allows detecting more subtle differences among species. Furthermore, a single framework for a taxon not only allows separate analysis of the risks from ecological stressors associated with the hazard of climate change (CC) and those associated with fishing and 'other anthropogenic' (FO) hazards but also of the risks from the CC and FO stressors acting together.

Within the one framework, we evaluate the risk of a marked reduction of each species' population using available information and data on its biology and environment and current understanding of its exposure to CC and FO anthropogenic hazards. We treat a species' vulnerability to each of CC and FO stressors independently, with risk

defined as the product of the degree of exposure to stressors and the resilience risk intrinsic to the species. We assign each species to one of six ecological groups based on lifestyle and habitat and then assess each group's exposure to CC and FO stressors. Attributing risks to population reduction associated with FO stressors independently of those with CC stressors allows us to identify and relate risk factors intrinsic to a species to increased mortality from FO stressors and reduced habitat (i.e., habitat area or suitability) from CC stressors.

We apply the framework to assess each chondrichthyan species with ≥20% of its present distribution inside a study region of southern Australia in the Exclusive Economic Zone (EEZ), where climate change is progressively reducing temperate-water habitats. Overall, the rate of change is most rapid in shallower waters and declines with increasing depth on the continental slope. We consider 11 different scenarios: 2 past FO scenarios assumed mostly free of CC stressors (i.e., occurring during 2000–2006 and 2018), 3 groups of hypothetical future CC scenarios free of FO stressors (i.e. low, medium and high emissions), and hypothetically 6 (i.e., 2 x 3) possible future combinations of the 2 past FO and 3 future CC scenarios. For analysis, as we will explain, we treat 'other anthropogenic' hazards (i.e., non-CC and non-fishing hazards) as a single invariant form of fishing with maximum risk. Applying maximum risk is consistent with the precautionary principle because information on the area of their influence and their changes over time is lacking. Because many of the species we assess have a part of their distribution north of our study region, we demonstrate the differences in their vulnerability between the study region of southern Australia and the entire Australian EEZ for each of the two past FO scenarios. However, with the advance of climate change and the changing proportion of the species' distributions outside the study region, we confine risk assessment for future scenarios to the inside of the study region.

1.1 | Concepts of risk, resilience and vulnerability

Risk is the potential or probability of an adverse event, and risk assessment is the process of obtaining quantitative or qualitative measures of risk levels. When applied to a natural population, risk assessment usually involves determining the likelihood of falling below a specified size. Conversely, it can apply to a population explosion (Burgman et al., 1993). Risk assessment in resource management became formalized as fisheries policies began embracing Ecologically Sustainable Development and Ecosystem-Based Fisheries Management principles in the 1990s (Fletcher, 2005; Francis & Shotton, 1997). Initially, risk assessment formed part of highly-quantitative single-species stock assessments of targeted teleosts such as orange roughy (*Hoplostethus atlanticus*, Trachichthyidae) in New Zealand (Francis, 1992) and sharks such as school shark (*Galeorhinus galeus*, Triakidae) in southern Australia (Punt & Walker, 1998). Subsequently, semi-quantitative approaches to risk assessment emerged for evaluation of relative risks among data-poor species retained (targeted and by-product species) or discarded by fishers (by-catch species) (Hobday et al., 2011; Stobutzki et al., 2002; Walker, 2005; Zhou et al., 2011). Some of these later approaches for assessing the risks from fishing also apply to threatened, endangered and protected species, habitats, and ecological communities (Hobday et al., 2011; Williams et al., 2011). Similar approaches also apply to climate change effects on chondrichthyan species (Chin et al., 2010) and harvested species of mixed taxa (Johnson et al., 2016; Pecl et al., 2014).

Regardless of location, species composition or types of fishing, meeting ecosystem objectives in fisheries management requires broad-scale monitoring, setting biological reference points (usually expressed in relative biomass), and selecting indicators for use as quantitative performance measures (Sainsbury et al., 2000). However, in practice, target and limit reference levels are mostly applied to economically valued species. The prohibitive costs and impracticality of assessing every species associated with whole-of-ecosystem management led to using indicator species. Indicator species enable the determination of risks to assemblages of biologically or ecologically similar species susceptible to fishing capture. Apart from their economic importance, indicator species are chosen based on their 'inherent vulnerability' (synonymous with 'resilience risk' in our framework) as determined from biological and ecological attributes (Newman et al., 2018). Where multiple lines of evidence are needed to identify particular species or parts of an ecosystem that may be at risk, the risk assessment process needs to have formal, transparent decision-making processes with broad stakeholder participation. The implementation of this approach is well advanced in the state of Western Australia. There, even if a model-based assessment of stock status is available, it becomes only one of the lines of evidence in a weight-of-evidence, risk-based approach to management (Fletcher et al., 2016). For example, this weight-of-evidence approach presently uses four indicator species of sharks as part of a process to assess ecosystem conditions and the stock status of all shark and ray species captured off Western Australia (Braccini et al., 2021).

The term 'vulnerability' is applied widely in science, engineering, economics, human health and public welfare. Common to these disciplines, vulnerability is the degree to which a system is likely to experience harm from exposure to specific stressors associated with hazards. Expressions such as vulnerability (or risk) analysis (or assessment) usually refer to processes identifying and prioritizing (or ranking) the risks in a system. The system can be an ecosystem or human community, at scales ranging from local to large regions (Adger, 2006; Füssel, 2007; Pickett et al., 2004; Smit & Wandel, 2006).

The Intergovernmental Panel on Climate Change (IPCC) applies the concept of vulnerability widely to its extensive and diverse scientific assessments of the causes, impacts and possible response strategies to climate change. It defines vulnerability as the degree to which a system is susceptible to and unable to cope with climate change's adverse effects, including climate variability and extremes (IPCC, 2007). A system's vulnerability is a function of the character, magnitude, and rate of climate change and variation in its exposure,

sensitivity and adaptive capacity. Sensitivity is the degree to which the system is affected, either adversely or beneficially, by climate change or variability. The effect may be direct, such as a change in crop yield in response to temperature change, or indirect, such as a change in inshore habitats in response to altered geomorphology caused by the increased frequency of coastal flooding following sea-level rise. Adaptive capacity is the system's ability to adjust to climate change, moderate potential damages, take advantage of opportunities or cope with the consequences of climate change.

The IPCC also widely applies the concept of resilience to ecosystems and human communities. Marine ecosystems are systems exposed to gradual changes and stochastic fluctuations in climate, ocean conditions, nutrient levels and geomorphology. Resilience is the capacity of an ecosystem or parts thereof, such as an ecological community or a species population, to resist alteration when exposed to abiotic or biotic stressors (Holling, 1973; Scheffer et al., 2001). Depending on the constancy (e.g., water temperature or ocean acidity) or stochastic perturbation (e.g., storm event or marine heatwave) of a stressor, biotic feedback processes enable the ecosystem to return towards its original state (resilience). If there is insufficient resilience, the ecosystem changes to an altered equilibrium state.

There is no consensus on the relationship between the concepts of resilience and vulnerability (Gallopin, 2006; Jannsen et al., 2006); nevertheless, we suggest there is a similarity between ecosystem resilience and the responses of populations to natural and anthropogenic stressors associated with climate change, fishing and 'other anthropogenic' hazards. Our method relies on the concept of resilience, where systems return to their original state with the easing of stressors, provided the effects of the stressors are not too strong. For FO stressors, the idea of resilience is consistent with the scientific paradigm underlying fish stock assessment. In the absence of fishing, a species' population size fluctuates about an average level in response to variation in natural environmental stressors. Over time, a balance persists between natural mortality, decreasing the population, and reproduction, increasing the population. Although the population reduces, it can adjust to a new balance between total mortality and reproduction if fished sustainably. Similarly, for CC stressors, the extent and suitability of habitat available to the population reduce and fluctuate about an average level in response to variation in natural environmental stressors. Given that most demersal chondrichthyan species presently confined to the continental shelf and continental slope off southern Australia have limited opportunity for poleward translocation, any increase in exposure to CC stressors will reduce population size by decreasing available habitat.

1.2 | Dynamics of populations in response to natural and anthropogenic stressors

Our analysis assumes that a marine ecosystem free of human influence over a specific period varies around a state of equilibrium. Each species' population size fluctuates both short- and long-term about that ecosystem's carrying capacity, depending on the stochastic variation in natural ecological stressors. The carrying capacity for each species depends on the suitable habitat and the resilience of the species. In this context, we consider the habitat to include the mix of ambient abiotic conditions and other species' presence in the ecosystem. A species' resilience relates to its persistence against changing abiotic and biotic stressors resulting from its competition with the other species for resources, its evasion of predators, its immunological responses to pathogens and disease, and its physiological and behavioural responses to periodic extremes in abiotic stressors. Typically, carrying capacity varies widely among species. Their relative population sizes range from small (rare species) to large (abundant species), where each species is part of one or more ecological communities. An ecosystem in a changed state of equilibrium most likely has its species composition and abundances altered. Driven by changing climate, ocean conditions, nutrients and geomorphology, abiotic stressors affect biotic stressors, leading to many species' changed abundances. The population size of an individual species varies naturally due to a mix of altered natural mortality and reproductive (birth) rates due to changes to its ambient physical-chemical environment and the populations of its predator, prey, pathogen, parasite and competitor species.

Anthropogenic stressors alter marine ecosystems by modifying natural abiotic and biotic stressors. For example, fluctuating water temperature is a natural abiotic stressor that can affect natural mortality or short- or long-term loss of a species' suitable habitat. Where the water temperature gradually rises from climate change, we refer to the temperature change, not temperature per se, as an anthropogenic stressor. Similarly, the natural mortality rate varies depending on many natural stressors; however, fishing increases the mortality rate and acts as an anthropogenic stressor by removing a portion of the population. Thus, we distinguish anthropogenic stressors from naturally occurring stressors and consider only anthropogenic stressors to assess resilience risk, exposure and vulnerability.

Anthropogenic stressors can have either positive or negative long-term effects on a species' population size, depending on the extent to which changing local conditions affect demographic, physiological and evolutionary processes. Species either cope or adjust to changing conditions by extending and contracting their geographic ranges through colonization and local extinction. Also, sub-lethal and lethal effects of stressors, such as temperature, impact populations at range edges when responses to stressors exceed physiological thresholds (Bates et al., 2014).

The degree of variation in stable population size and the response time to any perturbation in population size depends on the magnitude of the natural mortality and reproductive rates. In population dynamics models, these rates are often expressed jointly as the intrinsic rate of population growth. For *r*/*K* selection theory, these rates and the degree of inter-annual variation in population size are low for *K*-selected species, including all chondrichthyan species, despite differences in these rates among species. Conversely, natural mortality and reproductive rates and variation in population size are higher for *r*-selected species. They are particularly high, for example,

in cephalopod and coelenterate species and species of zooplankton. Highly *K*-selected species are long-lived with numerous age classes, produce relatively few surviving offspring annually, and exhibit comparatively stable populations in the absence of fishing but slow population growth during stock rehabilitation following depletion.

Age-based population-dynamics models applied to harvested shark species can illustrate how the pattern of stable population size at alternative levels depends on the magnitude of fishing mortality. Fishing mortality maintained at a low level allows the population to maintain a large size, whereas higher sustained fishing mortality over time causes the population to decline and to stabilize at a smaller size. As the instantaneous fishing mortality rate rises, reduced instantaneous natural mortality rate and increased reproductive and somatic growth rates are expected to maintain populations at smaller sizes. However, there is a level of fishing mortality beyond which the population fails to stabilize unless natural refugia or restrictions on using the fishing gear (e.g., mesh size or closed areas) protect part of the population. These patterns occur for two of southern Australia's historically most intensively studied and economically valuable species—the gummy shark (*Mustelus antarcticus*, Triakidae) (Pribac et al., 2005; Walker, 1994, 1998, 2010) and the school shark (Punt et al., 2000; Punt & Walker, 1998). These models demonstrate how the anthropogenic stressor of fishing, quantified as fishing effort (or fishing mortality), adds to the natural stressors in the ecosystem and reduces the population size. For the harvested population to remain in equilibrium (steady-state) at a reduced level in response to an increased mortality rate (natural mortality and fishing mortality rates combined), the total number dying over all age classes must balance the number of births. However, it takes many years for the population to equilibrate following a sudden change in fishing mortality.

Nevertheless, such models illustrate how biotic mechanisms provide stability, even though the actual mechanisms are more complex than those expressed in current models. For example, emerging evidence indicates that stability for several chondrichthyan species occurs with natural differences in reproductive rates associated with different environmental conditions in separate regions (Driggers & Hoffmayer, 2009; Walker, 2007; Yamaguchi et al., 2000) and years (Trinnie et al., 2016). There is also evidence of impairment of reproductive vitality in pregnant animals after escape or release following fishing-capture stress (Guida et al., 2017), which is likely to affect the reproductive output. Furthermore, the effects of capture stress can be intergenerational or transgenerational (Finotto et al., 2021).

The concept of resilience applies to vulnerability from exposure to stressors associated with anthropogenic hazards other than climate change and fishing (i.e., 'other anthropogenic' stressors), but various reviews use different terminology. One general review (Turner II et al., 2003) of ecological vulnerability analysis for 'other anthropogenic' stressors applies the three terms exposure, sensitivity and resilience, where resilience is the capacity of a system to cope with stressors. Another review (De Lange et al., 2010), which addresses the effects of hazardous chemicals in the environment, applies the terms exposure, toxicological sensitivity and resilience, where the resilience of an ecosystem is either the magnitude of disturbance that it can absorb before its structure changes or a measure of resistance to a disturbance. Replacing the term 'resilience' in these two reviews with 'adaptive capacity' would make their terminology consistent with that of the IPCC for climate change stressors and with ours for climate change, fishing and 'other anthropogenic' stressors.

1.3 | Aims of the present study

Our study has three aims. The first is to explain a method developed for identifying species of concern from the effects of anthropogenic stressors in the marine environment for mitigation, monitoring and research. The second aim is to apply the method for evaluating the resilience risk and vulnerability of chondrichthyan species to individual and combinations of anthropogenic stressors in southern Australian waters. As part of the second aim, we compare the vulnerability to fishing between southern Australia and the entire Australian EEZ. Our third aim is to describe how the method can be tailored for application to any other region of the world. We also offer advice on its application to taxa other than chondrichthyan species.

2 | MATERIALS AND METHODS

2.1 | Vulnerability analysis framework

2.1.1 | Vulnerability to fishing and climate change stressors

We determine risk from anthropogenic stressors in the marine environment for only those chondrichthyan species that have ≥20% of their present distributions in the Australian EEZ inside the boundary of our study region of southern Australia (Figure 1). Furthermore, we do not attempt to identify those species presently inside the region that are gaining competitive advantage and increasing their populations due to anthropogenic stressors. As the marine waters warm with advancing climate change, more northern distributed species around Australia will increasingly extend their distributional ranges southwards (Bates et al., 2014; Pecl et al., 2014) into our study region of southern Australia. However, we do not attempt to identify or assess the immigrating species with presently <20% of their distributions in the study region. That would require one or more additional study regions and extending the scope of the present study. These additions would increase the number of species, create additional data demands, and add the need to extend the coverage of temperate waters to include Australia's tropical and subtropical waters. Nevertheless, the methods we describe could apply to northern Australia by compiling the appropriate data and information.

Our risk measures relate to a 'marked reduction in population size' through increased mortality from FO stressors or reduced habitat from CC stressors. A marked reduction in population size is our criterion for harming a species. The magnitude of a marked

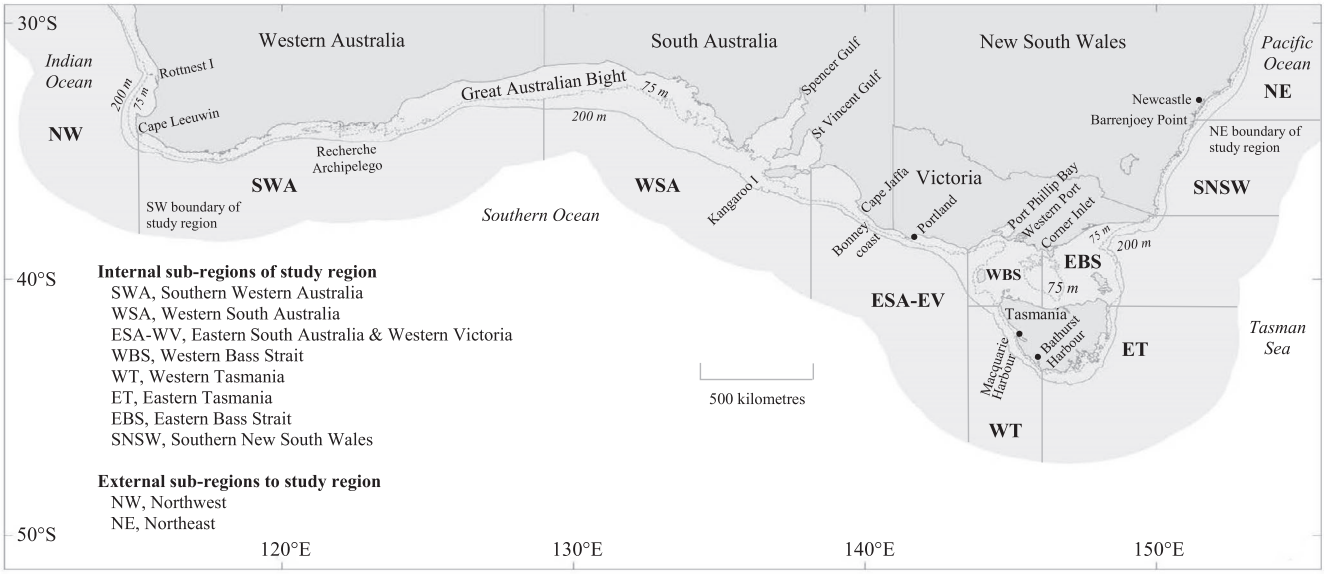

FIGURE 1 Study region of southern Australia and its internal and southern parts of external sub-regions within the Australian Exclusive Economic Zone boundary

reduction is of the order of the change in population size from the unfished level to the relative level required to maintain the maximum sustainable yield. The relative level varies depending on the species population productivity (Section 2.2.9).

We define vulnerability as the risk of marked population reduction for a species. Vulnerability to CC stressors is the product of the species' exposure (a component in common with the other species of its ecological group), and its resilience expressed as the product of two separate components (Johnson et al., 2016)—sensitivity and adaptive capacity (hereafter 'adaptability')—to those stressors. Thus, we adopt the widely-used equation

$$\text{Vulnerability} = \text{Exposure} \times \text{Sensitivity} \times \text{Adaptability}$$

as applied for CC stressors to the Great Barrier Reef's chondrichthyan fauna of north-eastern Australia (Chin et al., 2010). This exposure–sensitivity–adaptability framework (ESA) explicitly separates the exposure component, extrinsic to the species and potentially manageable by limiting global greenhouse gas emissions, from the sensitivity and adaptability components, which are both intrinsic to the species. By relating each of the three independent components of exposure, sensitivity and adaptability to risk and determining that risk, then their product provides an estimate of vulnerability expressed as risk.

For vulnerability to fishing stressors, we adapt productivity–susceptibility analysis (PSA), which forms a semi-quantitative part of the hierarchically structured framework referred to as Ecological Risk Assessment for the Effects of Fishing (Hobday et al., 2011). We retain the component productivity unchanged for our approach but alter the method of determining productivity risk (Section 2.2.9). On the other hand, we reformulate the component susceptibility. In PSA, susceptibility derives from the concept of catchability (q), a parameter used widely in fish stock assessment, usually defined as the proportion of a fished population killed by one unit of fishing effort and equals the ratio of instantaneous fishing mortality rate (F) to the fishing effort (f), i.e.,

$$F = qf.$$

Susceptibility in PSA for a type of fishing is the product of four other parameters, that is susceptibility = availability x encounterability x selectivity x post-capture mortality (Hobday et al., 2011; Walker, 2005). Availability for the fishing type is the proportion of the area of the spatial distribution of a species fished. Encounterability is the proportion of the available part of the population encountering the fishing gear, which relates to a species' mobility and vertical distribution in the water column relative to the moving or stationary fishing gear's vertical influence. Selectivity is the population's proportion encountering the gear selected and held captured (or impaired) by the gear. We alter the term post-capture mortality (Hobday et al., 2011; Stobutzki et al., 2002; Walker, 2005) to post-encounter mortality, which is the proportion of the selected part of the population that dies as a result of encountering the gear. Post-encounter mortality results from the trauma of capture when the animal is present in the fishing gear, or after it drops out or escapes from the gear, or after retrieval of the gear following handling trauma when discarded live. It can also be caused by the fishers killing the animal, either for their use, marketing, or before discarding it (Dapp et al., 2016).

For vulnerability analysis, we expand the term availability in PSA susceptibility, defined by the proportion of the spatial distribution of a species population (intrinsic to the species) overlapping the spatial distribution of the deployment of a fishery's fishing gear (extrinsic to the species). In a risk assessment framework, the population's risk is higher inside the fishing operations range than outside that range,

making it necessary to specify explicitly the region to which estimated risk levels apply.

Distinguishing risk levels among separate regions is particularly relevant to our study. Exposure of chondrichthyans to the two most intensive fishing types (demersal trawl and demersal shark gillnet) during our two chosen past fishing scenarios (2000–2006 and 2018) was high or medium inside the study region but mostly low or nil outside (see Section 2.2.11 for exceptions). Thus, for each scenario, we present risk estimates for our study region in southern Australia's waters and the entire EEZ of Australia (i.e., the full range of Australian jurisdiction). Low or nil exposure to fishing in the waters north of the study region provides large natural refugia for many of the species we assess. However, although it is reasonable to assume each of the two past fishing scenarios persists through the present century, climate change stressors can alter the risk (vulnerability) of population reduction in two ways. One is from a species' reduced natural refugia as its population shifts gradually southwards into the study region where conditions are more suitable, but fishing exposure is higher. The other is by altering the extent and suitability of the species' habitats.

To determine risks for both our study region and the Australian EEZ and to separate elements of susceptibility extrinsic and intrinsic to the species, we expand the term availability in PSA susceptibility as the product of the component exposure and the new susceptibility term 'regionality', such that

$$\text{Availability} = \text{Exposure} \times \text{Regionality}.$$

Each species has its own availability and regionality, whereas exposure applies to all species in its ecological group. Extrinsic to a species, exposure is the proportion of its distribution available (i.e., exposed in common with the other species of its ecological group) to fishing within the study region. Regionality is the proportion of a species' full spatial distribution in the Australian EEZ enclosed inside a prescribed region (e.g., study region, as for the present study, or one or more parts of that region) and required to allow treating exposure at the level of the ecological group.

Another reason to identify regionality as a distinct term (parameter) of susceptibility is that, for a species distribution straddling the study region and the more northern waters in the EEZ, its value will progressively approach 1 as its population redistributes southwards in response to climate change. For our study, regionality is known for past fishing scenarios, enabling the determination of vulnerability for not only the study region but the entire Australian EEZ, separately, which, when compared, demonstrates the significance of refugia in reducing fishing vulnerability. However, because regionality's value will alter and is not readily estimable for a straddling species, vulnerability estimates for future scenarios need confining to the study region. Thus, for fishing vulnerability, we formulate a risk equation similar to ESA, with three components, such that

$$\text{Vulnerability} = \text{Exposure} \times \text{Susceptibility} \times \text{Productivity},$$

where susceptibility, with all its terms intrinsic to the species, becomes

$$\text{Susceptibility} = \text{Regionality} \times \text{Encounterability} \times \text{Selectivity} \times \text{Post - encounter mortality}.$$

The exposure–susceptibility–productivity (ESP) formulation separates the extrinsic component of exposure from the intrinsic components of susceptibility and productivity. For past fishing scenarios, when determining the vulnerability of a species straddling inside and outside the study region, regionality is 1 for the study region alone but <1 for the Australian EEZ. However, for future scenarios, regionality is 1 in the study region, and we avoid assessing future vulnerability in the whole EEZ. This approach allows determining vulnerability separately for part of the EEZ, such as the study region for our analysis, by defining its boundary and setting its regionality to 1 when determining a species' vulnerability within the study region alone.

2.1.2 | Vulnerability to 'other anthropogenic' stressors

We pool all 'other anthropogenic' stressors (i.e., other than CC and fishing stressors) and treat these stressors jointly as a single type of fishing impacting the chondrichthyan populations as fishing mortality (i.e., anthropogenic mortality). Pooling these numerous, mostly under-studied, stressors provides for simple treatment of multiple impacts on a species ranging from mild to potentially lethal. Two studies evaluating risks from anthropogenic stressors to the biota in the Spencer Gulf of South Australia, which forms one small part of shelf-inshore waters within the boundary of our study region, illustrate the complexity of evaluating 'other anthropogenic' stressors. One study identified a total of 38 threats to 8 separate marine habitats (i.e., 304 threat-habitat combinations), where CC- and 'other anthropogenic'-related threats ranked as higher risk than threats related to fishing (Doubleday et al., 2017). The other study identified 27 threats to 38 threatened, protected and iconic marine-associated species, where fishing posed the greatest threats to elasmobranch species (Robbins et al., 2017).

Our analysis of chondrichthyan species does not account explicitly for the sub-lethal physical, physiological, immunological or genetic impairments to animals (Wheeler et al., 2020) in a species' population incurred from 'other anthropogenic' stressors, other than through reduced fitness increasing mortality. The analysis accounts for only mortality over and above natural mortality (i.e., anthropogenic mortality), reducing population size. Thus, as with fishing stressors, a species' adaptive capacity to cope with added mortality from 'other anthropogenic' stressors depends on its intrinsic capacity to adjust its natural mortality and reproductive rates through biotic, density-dependent compensatory-dispensatory mechanisms. Thus, we relate these mechanisms' effectiveness to the species' productivity risk (Section 2.2.9).

Applying the precautionary principle by assuming maximum risk with a lethal consequence (i.e., the risk is 1) to exposure and each

susceptibility attribute (i.e., regionality, encounterability, selectivity and post-encounter mortality) simplifies but inevitably overestimates the vulnerability. This over-estimation is not an issue for chondrichthyan species because most 'other anthropogenic' stressors occur inshore, affecting only the inshore ecological group, which has only one species. However, vital to our analysis is that inshore 'other anthropogenic' stressors, together with CC stressors, potentially reduce the critical habitat of six species allocated to offshore ecological groups but have nursery areas inshore (Section 2.2.9).

2.1.3 | Exposure analysis

As the product of resilience risk and exposure, vulnerability can be two separate independent analyses. Resilience risk analysis requires identifying and evaluating risk factors intrinsic to the species. In contrast, exposure analysis requires identifying and assessing the distribution and severity of stressors to the species that alter its population size.

Exposure analysis can be as simple as making broad-scale estimates of the overlap of the spatial distributions of ecological groups and the anthropogenic stressors from maps as in our study depending on the anthropogenic scenario. On the other hand, exposure analysis can involve detailed spatial risk assessments accounting quantitatively for specific habitats relative to the stressors' distributions and intensity. Such assessments include those applied to individual species and groups of colonial-nesting seabird species for present threats in eastern Canada (Lieske et al., 2020) and marine mammals at high risk of extinction from fishing in parts of the Gulf of Thailand and the South China Sea (Hines et al., 2020). In another example, spatial risk analysis demonstrates the effects on catches from the Tasmanian rock lobster fishery and the habitat suitability of southern rock lobster (*Jasus edwardsii*, Palinuridae) from exposure to future projected changing near-shore water temperatures, winds and currents (Pecl et al., 2009). The analysis investigates the trade-offs between (a) the potential gains from faster somatic growth rates and increased predation by the presence of larger rock lobsters reducing survival of sea urchins (*Centrostephanus rodgersii*, Diadematidae) and (b) the potential losses from reduced distribution and survival of phyllosoma larvae in warmer waters and reduced settlement of puerulus larvae resulting from the damaging effects of sea urchins on rock lobster habitats by denuding reefs of seaweed.

The component exposure varies with time depending on the scenario of CC, FO or a combination of CC and FO stressors and is controllable by limiting or eliminating the anthropogenic stressors. For our analysis, exposure also varies spatially. To account for species with part of its population north of our study region moving south in response to climate change, we assess risks for the two past FO scenarios in our study region of southern Australia and the entire Australian EEZ. To assess future vulnerability to stressors as climate change progresses, we hypothetically assume three separate FO scenarios (i.e., those observed during 2000–2006 and 2018, and no fishing) persisting through the present century for each of three CC scenarios (i.e., low, medium and high emissions). Although the FO scenario stressors can be assumed hypothetically to remain fixed into the future, the CC scenarios' stressors will change spatially and temporally in response to gradual processes and stochastic events, causing less predictable mosaic patterns of continuously changing habitats.

2.1.4 | Resilience risk analysis

The component exposure, extrinsic to the biology of species, varies in time and space depending on the scenario of CC, FO or a combination of CC and FO stressors and is controllable by limiting or eliminating the anthropogenic stressors. The components of sensitivity, adaptability, susceptibility and productivity, on the other hand, vary less temporally and spatially and are intrinsic to a species' biology and variously determine each species' resilience to anthropogenic stressors. Although we view susceptibility as a form of sensitivity and productivity as a form of adaptability to FO stressors, we retain the original terms applied to PSA components. However, we follow other authors (Johnson et al., 2016) and view the product sensitivity × adaptability as resilience to CC stressors but also adopt the product susceptibility × productivity as resilience to FO stressors. We refer to these intrinsic components as resilience components and present resilience risk as part of our method's results. The potential risk is inherent to the species and independent of exposure to stressors associated with alternative anthropogenic scenarios.

Evaluation of each of the four resilience components requires identifying measurable characteristics treatable as risk factors. Such characteristics—attributes (Chin et al., 2010; Hobday et al., 2011; Pecl et al., 2014) or traits (De Lange et al., 2010)—variously relate to the biology of a species through its demography, morphology, phenology, physiology or lifestyle. We treat selected attributes as continuous or categorical variables for calculating risk. For FO stressors, the susceptibility and productivity components relate to a species' mortality and reproductive rates. For climate change, the sensitivity and adaptability components relate to a species' range of habitats. Although FO stressors can alter habitats, we assume that the effects of changed habitat on population size are small compared with the more direct effects of removing or adding animals from changed mortality and reproductive rates. Also, although periodic events related to climate change can cause changed mortality and reproductive rates over short periods, our method assumes that these periodically changed rates are low compared with the effects of altered habitats in the long term. The assumption that marked reduction in population size from FO stressors is attributable only to changed total mortality and from CC stressors is due to modified habitats in extent or suitability has two advantages. One is that the assumption reduces the complexity of the method. The other ensures that each attribute is applied to only a single resilience component, thereby

avoiding repeated use of the same information or data for different parts of the analysis.

We treat each attribute as a single risk factor for our analysis, except for the four attributes of susceptibility (regionality x encounterability x selectivity x post-encounter mortality). Their product combines to form a single risk factor. The risk associated with each risk factor is within the range 0–1, where 0 is no risk, and 1 is the maximum possible risk. Each resilience component's risk value is also in the range 0–1, calculated from the risks associated with individual attributes. The resilience risk rises with increasing sensitivity and susceptibility but declines with increasing adaptability (Chin et al., 2010) and productivity (Hobday et al., 2011; Walker, 2005). In other words, high sensitivity and high susceptibility are high risks, whereas high adaptability and high productivity are low risks. Conversely, low sensitivity and low susceptibility are low risks, whereas low adaptability and low productivity are high risks. Given that exposure is the proportion of the spatial area inhabited by a species subjected to the anthropogenic stressors and vulnerability=exposure × resilience risk, both exposure and vulnerability are also within the range 0–1. Any rise in exposure increases vulnerability, and conversely, any reduction in exposure decreases vulnerability.

2.2 | ESA–ESP analysis and its 12 steps

We refer to our method as exposure–sensitivity–adaptability and exposure–susceptibility–productivity (ESA–ESP) analysis. Treating vulnerability to CC and FO stressors in the same way within the one analytical framework has the key advantage of allowing separate analyses of exposure and resilience risk as well as amalgamating them for vulnerability analysis applied to any range of CC, FO and CC-FO combined scenarios. Importantly, the framework facilitates the presentation of risks calculated deterministically for each species from all anthropogenic stressors at the levels of risk factor, resilience and vulnerability.

In summary, ESA–ESP analysis adapts, broadens and combines appropriate existing methods in a 12-step generalized method to evaluate risk factors and the resilience risk of species to all anthropogenic stressors in the marine environment. Moreover, the method can evaluate vulnerability for any past, present, envisaged or potential mitigation scenario for any selected region (Table 1). ESA–ESP analysis has a risk-hazard framework but does not account for risk from rare catastrophic disasters of natural origin (e.g., seismic disturbance or extra-terrestrial impacts) or anthropogenic origin (e.g., mining, hydrocarbon extraction or transport accidents). ESA–ESP analysis is biophysical and geocentric because it focuses on spatially-based stressors associated with anthropogenic hazards modifying natural abiotic and biotic stressors' magnitude. ESA–ESP analysis provides a standard format for arranging information and data as input to the analysis and presenting risks from anthropogenic stressors for any assemblage of species; it is particularly suitable for relatively *K*-selected species.

Supporting information for several of the 12 steps of the methods is presented in four of five appendices in Supplementary Material 1; the fifth appendix provides a brief history of fishing impacts and prognosis for chondrichthyans of southern Australia using the results of our ESA–ESP analysis. Additional supporting information on the methods and results appears as two figures and

TABLE 1 Twelve steps for ESA–ESP analysis of chondrichthyan species to anthropogenic stressors

Step no.	Procedure
1	Identify boundaries of the jurisdiction (for species management or other purposes) and study region.
2	Describe geographic features, bathymetry and substrates of the study region.
3	Describe oceanography of the study region.
4	Identify scenarios for evaluating anthropogenic stressors.
5	Identify recent and potential oceanographic and ecological changes for alternative CC emissions scenarios.
6	Identify chondrichthyan species with ≥20% of Australian distribution inside the study region.
7	Identify ecological groups for categorizing species according to lifestyle and habitat.
8	Identify anthropogenic stressors in the study region.
9	Identify species attributes as resilience risk factors and develop methods for evaluating risk.
10	Evaluate species resilience risk for each risk factor to CC, FO and combined CC-FO stressors.
11	Evaluate exposure of each ecological group to stressors for each CC and FO scenario.
12	Evaluate species vulnerability for each CC, FO and combined CC-FO scenario.

Note: CC, climate change; ESA–ESP, exposure–sensitivity–adaptability and exposure–susceptibility–productivity; FO, fishing and 'other anthropogenic' stressors.

11 tables in Supplementary Material 2. All information and data used as input to the ESA–ESP analysis are from the cited literature or contained in three supplementary tables. Tables S1 and S2, respectively, summarize data and provide separate references for dietary and aging studies of chondrichthyans at the level of species or higher taxa. Table S3 collates and arranges the summary diet and age data and other data types for each species as input to the analysis.

2.2.1 | Jurisdictional and the study region boundaries

We designed our study to inform agencies with management responsibility and bodies interested in the Australian EEZ's chondrichthyan fauna. Our ESA–ESP analysis applies to each chondrichthyan species, with ≥20% of its spatial distribution inside our study region in the EEZ's southern part. Although the value is arbitrary, it recognizes that species with <20% of their distributions present are at low vulnerability from the anthropogenic stressors in our study region and best assessed by separate studies. As mentioned, each species' regionality is its spatial proportion of a species' distribution inside the Australian EEZ occurring in the study region of southern Australia. However, those species with part of their distributions occurring outside the Australian EEZ would have lower regionality values for an ESA–ESP analysis extended to a broader region of interest, such as Australasia, the Southern Hemisphere or the world. Conversely, recognizing that fishing risk can vary spatially, an ESA–ESP analysis can assess the risk separately for any part of the study region by setting regionality for that part to 1. Thus, defining the study region's boundaries relative to any broader region of jurisdictional or general interest is an essential first step of ESA–ESP analysis for assessing vulnerability to FO stressors.

Our study region of southern Australia (Figure 1) covers the contiguous spatial areas prescribed in legislation for the Great Australian Bight Trawl Sector and the Commonwealth Trawl Sector of the federally managed Southern and Eastern Shark and Scalefish Fishery. The region includes a trawl-exclusion area west of longitude 125.08°E in waters of depth <200 m adjacent to the south coast of Western Australia. In addition to demersal trawl (otter trawl and Danish seine), the region encompasses other fishery sectors that deploy gillnets, hooks and traps. However, the region excludes the more northerly distributed East Coast Deepwater Trawl Sector (Georgeson & Curtotti, 2020) and Western Deepwater Trawl Fishery (Butler & Steven, 2020). Hence, our study region is that portion of Australia's EEZ between Cape Leeuwin (longitude ~115.13°E) on the southern coast of Western Australia and Barrenjoey Point (latitude 33.58°S) on the eastern coast of New South Wales. Within the 200-NM boundary from shore, this region also includes the state-managed fisheries of South Australia, Victoria, Tasmania, the southern region of New South Wales, and the south coast of Western Australia. The study region is ~2 million km^2 and includes a broad range of marine ecosystems.

2.2.2 | Geographic features, bathymetry and substrates of the study region

Depths in the region range from near-shore shallows across a mostly narrow continental shelf, which widens eastwards on the south coast of Western Australia and western South Australia and in Bass Strait (Figure 1). A comparatively steep continental slope (~200–4,000 m deep) bounds the continental shelf's outer edge and leads to the abyssal plain's vast expanse with depths in the southwest up to 6,400 m and in the southeast up to 4,600 m. The seafloor of the continental shelf, including the Bass Strait, has widespread soft sediments interspersed with rocky reefs, and the continental slope has extensive plateaus, canyons and stepping escarpments, many of which connect with the abyssal plain. South and east of Tasmania, seamounts rise from the abyssal plain to heights of mostly 2,000–4,000 m, and the South Tasman Rise reaches from the seafloor to heights of ~1,500 m to ~750 m below the surface. The seamounts variously restrict and intensify the flow of deep ocean currents that inhibit the accumulation of sediment. The regional topography and isolation from other landmasses have led to high endemism of the fauna, including chondrichthyans.

To evaluate the risk for the species attribute 'distributional flexibility' (Section 2.2.9), we divide the study region of southern Australia into eight sub-regions). These sub-regions are Southern Western Australia (SWA), Western South Australia (WSA), Eastern South Australia and Western Victoria (ESA-WV), Western Bass Strait (WBS), Western Tasmania (WT), Eastern Tasmania (ET), Eastern Bass Strait (EBS), and Southern New South Wales (SNSW) (Figure 1). The rationale for these sub-regions relates mostly to the ocean currents and upwelling affecting water temperatures. Several studies refer to latitude range as a species attribute (Chin et al., 2010; Pecl et al., 2014), but although this could apply to SNSW, EBS and ET, water temperature also varies across southern Australia longitudinally. Furthermore, to account for the full distribution of species occurring both within and outside the study region, we add two external sub-regions—northwest (NW) and northeast (NE)—divided at Cape York in northern Queensland.

2.2.3 | Oceanography of the study region

The Australian mainland and three oceans (Indian, Southern and Pacific) bound the study region (Figure 1). There is a gradient from warm-temperate waters abutting the mainland to cool temperate waters in Bass Strait and around Tasmania (latitudes ~38–45°S) and progressively colder bottom water with increasing depth across the continental shelf, down the continental slope, and onto the abyssal plain.

Surface waters on the continental shelf and at the shelf break off southern Australia, unlike waters around other continents, are dominated by two warm-water currents (Leeuwin and East Australian Currents) transporting polewards low-nutrient water from

tropical and subtropical regions (Appendix S1). The cold Antarctic Circumpolar Current flows eastwards through the southern part of the study region. In contrast, the cool subsurface Flinders Current flows westwards along the continental slope from Tasmania to Western Australia and then beneath the Leeuwin Current towards the equator. Flowing most actively near the 600-m isobath, the Flinders Current contributes to upwelling and downwelling within the many canyons on the region's continental slope, which affect demersal water temperatures on the continental shelf and slope. The conditions associated with the mix of warm and cold ocean currents, upwelling and downwelling, and the three depth zones of the ocean stratified by water density influence the bathymetric distribution of the chondrichthyan fauna and their habitats within the study region.

2.2.4 | Anthropogenic scenarios for evaluating risks to CC and FO stressors

The science of climate change requires envisaging possible alternative environmental futures based on projected alternative emissions scenarios. Climate models integrate the climate system's interacting parts (atmosphere, hydrosphere, cryosphere, land surface and biosphere) (Moss et al., 2010). The IPCC emissions scenarios developed most recently relate directly to the radiation imbalance in the earth's atmosphere, causing mean global temperatures of air at the earth's surface to rise. These scenarios, referred to as Representative Concentration Pathways (RCPs), are named according to radiative forcing expressed as W m^{-2} in the upper atmosphere predicted for the year 2100. In the RCP8.5, radiative forcing continues rising after the atmosphere's greenhouse gases reach a CO_2 equivalent concentration of 1,313 ppm in the year 2100. The RCP6.0 and RCP4.5 stabilize after 2100 at ~800 ppm and ~630 ppm, respectively, and the RCP2.6 peaks at ~3 W m^{-2} with 475 ppm before the year 2100 and then declines (IPCC, 2013b). Adherence to the agreement signed by nearly 200 countries since the 2015 United Nations climate conference in Paris to restrict the rise in the global mean surface temperature of the air to less than 2.0°C, while aiming to maintain it to below 1.5°C, provides a trajectory above the RCP2.6 but slightly below the RCP4.5 (IPCC, 2018).

To evaluate each chondrichthyan species' exposure to CC stressors in the marine environment, we categorized these RCPs and several other commonly used scenarios as low, medium and high emissions. This categorization provides a basis for assembling information from the literature on projections of the CC stressors through to the year 2100 for each of our three broad categories of greenhouse gas emissions scenarios (Table S4). Although standard emissions scenarios have smoothly changing radiative forcing and CO_2 equivalent concentration predicted to the year 2100, and beyond, the loss of suitable habitat for chondrichthyans does not progress smoothly. Gradually increasing CC stressors, emerging hotspots, and stochastic extreme events such as marine heatwaves and storms will inevitably create a mosaic of altered habitats where much of the study region will be changed irreversibly long before the year 2100. Thus, rather than defining future scenarios for species exposure to CC stressors according to any specific year, we simply refer to low, medium and high emissions scenarios as the emissions progressively increase into the future.

We evaluate the risks of exposure to FO stressors, on the other hand, during two periods in the past separated by a decade of significant fisheries management reform. The first period was 2000–2006 when demersal trawl effort peaked, and the second was the year 2018, by which time fishing effort had halved and spatially contracted for each of demersal trawl (Emery et al., 2020; Moore et al., 2020) and demersal shark gillnet fishing (Woodhams et al., 2020). Exposure to 'other anthropogenic' stressors (i.e., other than fishing and CC stressors) treated as a single form of fishing is assumed not to have changed between the two periods because of insufficient data to evaluate a change. For assessing each species' vulnerability, we adopt two FO scenarios (i.e., the past 2000–2006 and 2018 periods, assuming the absence of CC stressors) and three CC scenarios (i.e., low, medium and high emissions, assuming the absence of FO stressors). Also, given that it is not feasible to predict FO stressors for the distant future, we combine the two FO scenarios separately with each of the three CC scenarios to produce six FO-CC scenarios. These six hypothetical scenarios plus the two past FO and three future CC scenarios give 11 scenarios.

2.2.5 | Potential oceanographic and ecological changes for alternative emissions scenarios

Warming of the oceans globally during 1971–2000 averaged 0.11 (0.09–0.13)°C per decade in the uppermost 75 m, decreasing progressively to 0.040°C per decade at 200 m, and 0.015°C per decade at 700 m (IPCC, 2013a). Regional climate models of high resolution developed for Australia translate the large-scale weather and ocean dynamics from global climate models to provide future projections of sea surface temperature (SST) and other variables (Hobday & Lough, 2011). Projected rises above 1986–2005 in median SST (with 80% prediction intervals) around Australia by 2080–2099 are 0.67 (0.31–1.13)°C, 1.28 (0.87–1.84)°C and 2.67 (2.04–3.70)°C for low, medium and high emissions scenarios, respectively (Table S4). The increases vary spatially, such that within our study region, SST rises off southern parts of Western Australia, and from NSW to southern Tasmania are among the highest. The lowest increase is of the southern mainland coast's central parts (Lenton et al., 2015). The models indicate that during all seasons, the rate of warming has accelerated, most notably off south-western and south-eastern Australia, where climate zones exhibit a southward shift of ~100 km on the western coast and >200 km on the eastern coast (Lough & Hobday, 2011). These changes in abiotic conditions are already producing periodic extremes and widespread ecological changes (Appendix S2).

Climate change is altering water density, temperature variation and the strength of the ocean currents, upwelling and downwelling.

Coupled with climate cycles such as the El Niño–La Niña and decadal cycles in the Pacific Ocean, the Indian Ocean Dipole and the Antarctic Oscillation, these changes create more extreme oceanographic and weather events. With associated rising water levels and shoreline inundation from thermal expansion and global ice melt, such changes have destructive flow-on effects such as increasing storm frequency and intensity. Patterns of ocean acidification, nutrient availability, coastal geomorphology, rainfall and freshwater run-off are also changing. Together these abiotic changes affect habitats and the productivity of ecosystems.

Changing patterns throughout southern Australia of upwelling and freshwater run-off, together with rising water temperature, ocean acidity and UV light radiation, as in other parts of the world, will alter primary production and trophic and competitive relationships among species. As tropical phytoplankton species gradually replace temperate species, the more productive temperate species' distribution is projected to occur only in a small area west of Tasmania. Although phytoplankton relies on dissolved carbon dioxide, increasing acidity will reduce calcification and quality of calcitic shells of certain species of phytoplankton, zooplankton and other taxa (Hobday et al., 2006). Ecological modelling projections under high emissions scenarios indicate that the proportions of phytoplankton, jellyfish and small pelagic teleosts in south-eastern Australia will rise; however, zooplankton, mesopelagic species and certain benthic invertebrates will decline. Sharks may increase in the short term but will then fall (Fulton, 2011). Other ecosystem modelling shows that lower-trophic-level consumers respond more to primary production than high-trophic-level consumers (Watters et al., 2003).

2.2.6 | Chondrichthyan species with ≥20% of Australian distribution in the study region

Information for each species on the local common name, taxonomic classification, and spatial and bathymetric distribution within the Australian EEZ was from the taxonomic guides in Australia for the sharks and chimaeras (Last & Stevens, 2009) and the rays (Last et al., 2016). Subsequent name changes are based on Fishes of Australia (Bray & Gomon, 2020) and advice from Dr William White of CSIRO National Collections and Marine Infrastructure (personal communication). Recent authorities moved the genera *Apristurus*, *Asymbolus* and *Figaro* from the family Scyliorhinidae to Pentanchidae and the grey nurse shark (*Carcharias taurus*) from the family *Odontaspididae* (sand sharks) to Carchariidae (grey nurse sharks). We treat Ogilby's ghostshark (*Hydrolagus ogilbyi*, Chimaeridae) and the blackfin ghostshark (*H. lemures* synonymized as *Chimaera ogilbyi* (Chimaeridae) (Finucci et al., 2018) as separate species for our analysis using the names *Chimaera ogilbyi* (syn *H. ogilbyi*) and *C. ogilbyi* (syn *H. lemures*), respectively. The original separation as species was based on morphology, whereas genetic and more recent morphological information indicates a single species.

2.2.7 | Ecological groups for categorizing species according to lifestyle and habitat

Assigning the chondrichthyan species assessed by the study into a small number of ecological groups (EGs) reduces the complexity of evaluating each species' exposure to anthropogenic stressors. Sufficient EGs must cover the region's entire area and categorize every chondrichthyan species selected for inclusion in the ESA–ESP analysis.

For southern Australia, exposure to anthropogenic stressors tends to decline with increasing ocean depth and varies depending on the type of substrate and presence of ocean currents, upwelling and downwelling. The tendency for chondrichthyan species to separate into taxonomic assemblages within broad bathymetric ranges provided initial criteria for defining EGs. The clear distinction between demersal (including benthopelagic) and pelagic species provided an additional criterion. The prohibition of most fishing ≥700 m depth since 2007 enabled defining an EG comprising deep-sea species that are now mostly unfished, apart from negligible bycatch taken during spatially limited occasional seasons for targeting orange roughy.

We also adopted criteria based on differences in the types of fishing associated with targeting practices and the practicality of operating fishing gear on particular substrate types. These criteria include targeting pelagic versus demersal species, inshore versus offshore species, and species inhabiting hard substrates (reef and rubble) versus soft substrates (sand, silt and mud) on the seafloor, and differences in the bathymetric range of species assemblages. These criteria provided the basis for defining a total of six EGs. One EG is pelagic; three inhabit the continental shelf in depths <200 m (shelf-inshore, shelf-reef and shelf-sand), and two inhabit the continental slope and abyssal plain (bathyal-upper 200–699 m and bathyal-lower ≥700 m depth) (Table 2). Spatially, the pelagic EG covers the entire region. The bathyal-lower EG covers more than three-quarters of the region. The shelf-sand group covers most of the continental shelf. Although the shelf-reef, shelf-inshore and bathyal-upper EGs occupy much smaller areas, their habitats are critical for many of the chondrichthyan species.

2.2.8 | Anthropogenic stressors in the study region

We identified eight climate change stressors, five fishing types and seven 'other anthropogenic' stressors. 'Other anthropogenic' stressors are treated jointly as a sixth fishing type, which can reduce the size of a chondrichthyan species' population by increasing mortality or by reducing habitat suitability or extent. The eight CC stressors are rising (1) water temperature, (2) sea level, (3) ocean acidity, and (4) UV light intensity; decreasing (5) dissolved oxygen, and (6) freshwater run-off from land to the sea; increasing (7) storm frequency and strength; and changing (8) ocean currents, upwelling and downwelling. The seven 'other anthropogenic' stressors are (i)

TABLE 2 Ecological groups identified for categorizing species in preparation ESA–ESP analysis

Ecological group	Distributional criteria for categorizing species into ecological groups
Shelf-inshore	The species inhabit only nearshore areas, estuaries, bays, gulfs or inlets, where they encounter numerous stressors associated with recreational and artisanal fishing, climate change and 'other anthropogenic' hazards.
Shelf-reef	The species inhabit mainly rocky or rubbly hard substrates on the continental shelf in depths <200 m, where only the use of hooks occasionally occurs, and it is impractical to use either demersal trawl or shark gillnets without damaging the gear.
Shelf-sand	The species inhabit mainly sandy, muddy or silty soft substrates on the continental shelf in depths <200 m, where the use of demersal trawl and shark gillnets occurs without damaging the gear.
Bathyal-upper	The species inhabit mainly the upper continental slope in depths 200–699 m, where the use of demersal trawl occurs, but the use of demersal gillnets and hooks is negligible.
Bathyal-lower	The species inhabit mainly the continental slope in depths ≥700 m, which since 2007 has been closed to all types of fishing apart from occasional short-term demersal trawl seasons for orange roughy (*Hoplostethus atlanticus*, Trachichthyidae).
Pelagic	The species have a pelagic lifestyle in the waters from shore to the ocean 200-NM boundary of the Exclusive Exclusive Zone, where fishing effort from hooks and purse seine is low (catches of the species occasionally occur in demersal fishing gear).

environmental modification (e.g., port construction, channel dredging, beach renourishment, pipelines, and lost or dumped materials), (ii) artificial electric and magnetic fields underwater, (iii) artificial noise underwater (including seismic survey), (iv) artificial light underwater, (v) hydrocarbon and other chemical contamination, (vi) nutrient enrichment and (vii) invasive species. Although not required for identifying CC and 'other anthropogenic' stressors, identifying fishing stressors requires consideration of specific characteristics of fishing gear (e.g., selectivity) and its use (e.g., the bathymetric range, position in the water column or type of substrate for deployment).

Fishing stressors on populations of chondrichthyan species in southern Australia are from the targeted catch, by-product catch and by-catch, taken mostly in the offshore industrial fisheries by demersal trawl and demersal shark gillnet fishing. Comparatively, small catches occur in the inshore non-industrial fisheries by the recreational use of rod and reel and artisanal deployment of hooks, gillnets and seine nets from small boats and the shore. Similarly, low chondrichthyan catches occur offshore over small areas in the pelagic fisheries of midwater trawl, purse seine, squid machine jigging, pelagic longline and gamefish rod and line. The most significant of these fisheries are pelagic longline targeting tuna and billfish in the inner parts of the SNSW sub-region (Larcombe et al., 2020) and purse seine targeting southern bluefin tuna (*Thunnus maccoyii*, Scombridae) south of Kangaroo Island (Patterson et al., 2020) (Figure 1).

Based on the total catch of chondrichthyan species and the fishing methods, we categorized the fisheries into five types: non-industrial demersal inshore fishing (recreational and artisanal), industrial demersal trawl (including Danish seine), industrial demersal shark gillnet (legislated mesh size 150–165 mm), industrial demersal longline with baited hooks, and pelagic fishing (industrial and game). Other types of fishing, such as offshore demersal gillnetting for teleosts, pot fishing for decapods, and dredging and diving for molluscs, are known to take negligible catches of chondrichthyan species of southern Australia (Table S5).

Of a mean annual chondrichthyan catch of 6,467 t (live mass) during 2000–2006, taken by demersal trawl, hook and non-shark gillnet, estimated from an onboard observer program, most was by demersal trawl (97.1%) with small quantities taken by hook (2.8%) and non-shark gillnets (0.1%). Of an additional mean annual chondrichthyan catch of 4,767 t (live mass) reported by commercial fishers in mandatory logbook returns during 2000–2006, 76.2% was from the offshore industrial shark gillnet fishery, and 23.8% was from inshore demersal non-industrial fisheries. Significant by-catch of Port Jackson shark (*Heterodontus portusjacksoni*, Heterodontidae) and draughtboard shark (*Cephaloscyllium laticeps*, Scyliorhinidae) is from the shark gillnet fishery (Walker et al., 2005) and not reported in logbook returns. However, provided these species are treated with care and returned promptly to the water live, they survive (Frick et al., 2009, 2010). Catches of chondrichthyan species by pelagic fisheries were not closely monitored but are low given the low fishing effort in oceanic waters over the southern part of Australia's EEZ.

Although fishing effort from the industrial demersal longline fishery was negligible, it is one of the five fishing types listed for several reasons. Demersal longlines targeted sharks before the transition to demersal gillnet during the late 1960s and early 1970s (Walker, 1999). More recently, phasing out of demersal longline with automatically baited hooks for targeting teleosts reduced the catch of shark species taken as a by-product on the upper continental slope. However, there remains the option of reintroducing this method to target gummy sharks following the recent closure of large areas on the continental shelf off South Australia to the use of gillnets to improve the protection of sea lions (*Neophoca cinerea*, Otariidae) (Emery et al., 2020). A significant disadvantage of reintroducing demersal longlines is that it will encourage targeting large breeding females aggregating at particular sites in coastal waters. On the other hand, demersal gillnets with a legislated mesh size of 150–165 mm have the advantage of avoiding the capture of the smallest and largest animals in the population of gummy sharks, which facilitates robust management while ensuring the highest maximum sustainable yield (Walker, 2010).

Following >30 years of targeting gummy sharks and school sharks on the continental shelf and upper margins of the slope with

demersal shark gillnets, targeting school sharks declined with the adoption of a total allowable catch in 2001, designed to rebuild the stocks of this severely depleted species. These gillnets subsequently targeted mostly gummy sharks in depths <80 m where, during 2003–2004, 93% of the species' catch occurred (Walker & Gason, 2009). This change significantly reduced the area of deployment of gillnets. Of the continental shelf area inside our study region, 63% is <75 m, and 37% is 75–200 m deep.

2.2.9 | Determining risk from species attributes for each resilience risk factor

We modified some of the attributes applied for assessing risk from CC stressors to the chondrichthyan fauna of the Great Barrier Reef (Chin et al., 2010) to suit southern Australia's conditions. For sensitivity, we retained rarity and divided habitat specificity into three parts comprising three independent dependencies (reef-habitat, freshwater-habitat and inshore-nursery habitat with associated migration phenology), each of which relates to a specific ecological group. For adaptability, we dropped the attribute mobility because all southern species can move or redistribute in response to long-term or short-term changes in conditions unless they have specific habitat dependence. However, mobility is a relevant risk factor for invertebrate and teleost taxa. We combined latitude range and physical-chemical tolerance to form the single attribute distributional flexibility. In southern Australia, both latitude and longitude affect habitat suitability and thus the distribution of a species. We modified trophic specificity to adopt a measure of specialization on prey taxa at specific trophic levels to account for the higher risk of the cumulative effects of an ecological disturbance at the upper levels of the trophic pyramid than at the lower levels (Purvis et al., 2000).

For ESA–ESP analysis, the number of risk factors (each related to one or more attributes) (I) varied among the four resilience components of sensitivity (I = 2), adaptability (I = 2), susceptibility (I = 1) and productivity (I = 1). The two risk factors of sensitivity are rarity and habitat specificity. The two attributes of adaptability are distributional flexibility and trophic level. As the product of four parameters (i.e., attributes regionality, encounterability, selectivity and post-encounter mortality), susceptibility forms a single risk factor. Similarly, productivity forms a single risk factor.

To ensure that we could evaluate the risks associated with attributes treated as risk factors within the range 0–1 in a repeatable way, we assigned values using available information on each species (Table S3) according to a set of equations (Appendix S3) and decision rules (Table S6). Although the equations and decision rules embody the authors' subjective opinions, the rules are repeatable and potentially subject to refinement and application to subsequent resilience and vulnerability analyses by independent assessors as more information becomes available. Where information is inadequate for evaluating an attribute (i.e., no information or small sample size), we used a value calculated from one or more taxonomically related species. Otherwise, we applied the precautionary principle by assigning the maximum possible risk value of 1.

To test the sensitivity of the assigned and calculated risk values produced by the equations and decision rules, we first set base-case values for the decision rules and the equation parameters. We then varied each of these values over specified ranges, one at a time, to assess changes in the total numbers of species determined by ESA–ESP analysis at high (H) or medium (M) vulnerability.

2.2.10 | Resilience risk of species to CC, FO and CC-FO stressors

The risk value of each resilience component for a species is also in the range 0–1, calculated from the individual attributes treated as risk factors for the component using the equation

$$\text{Resilience component risk} = 1 - \prod_{i=1}^{I} (1 - p_i) \quad (1)$$

where I is the number of risk factors evaluated for the component (i.e., I is 1 or 2 for our study) and p_i is the risk contributed by the ith risk factor of the component.

We calculated the resilience risk intrinsic to each species from CC stressors, R_{CC}, by the equation

$$R_{CC} = \text{Sensitivity risk} \times \text{Adaptability risk},$$

from FO stressors, R_{FO}, by

$$R_{FO} = \text{Susceptibility risk} \times \text{Productivity risk},$$

and from CC and FO stressors acting together, $R_{CC\,\&\,FO}$, using the same formulation for combining risks as in Equation 1, by

$$R_{CC\&FO} = 1 - (1 - R_{CC})(1 - R_{FO}). \quad (2)$$

2.2.11 | Evaluate exposure of each EG to stressors for two FO and three CC scenarios

All species of an ecological group experience the same exposure to anthropogenic stressors. For the CC and FO stressors separately, we evaluated the exposure of the species and their habitats in an ecological group to the stressors as the proportion of the spatial area occupied by its EG exposed to the stressors, as either nil (N), low (L), medium (M) or high (H). We set N = 0.000 where the exposed proportion of the area was zero or negligible, L = 0.333 for >0 and <⅓ of the area exposed, M = 0.667 for ≥⅓ and <⅔ exposed, and H = 1.000 for ≥⅔ exposed.

With the one exception of the shelf-sand EG, exposure to the anthropogenic stressors is N or L (whichever makes no difference to our results) for that portion of the population of a species outside our study region in sub-regions NW (entire west and north coasts

of Australia to Cape York) and NE (entire east coast of Australia to Cape York north of sub-region SNSW). A small number of vessels are restricted to depths ≥200 m in the Western Deepwater Trawl Fishery (Butler & Steven, 2020) and East Coast Deepwater Trawl Sector (Georgeson & Curtotti, 2020). These fisheries began in the early 1990s to target orange roughy but have since applied either zero or little fishing effort. When determining the Australian EEZ vulnerability for each species in the shelf-sand EG in the NW sub-region south of latitude 26° S, we applied the value of regionality to account for the exposure to the industrial demersal shark gillnet fishing type (Braccini et al., 2021). In other words, we added the proportion of a species' distribution present in the southern part of sub-region NW (Table S3). This addition required dividing the NW sub-region into NW (South) south of 26°S and NW (North) north of this latitude in Western Australian and northern Australia eastwards to Cape York. Fishing effort is low in NW (North), which explains why regionality is <1 for four species. The four species are dusky shark (*Carcharhinus obscurus*, Carcharhinidae), pencil shark (*Hypogaleus hyugaensis*, Triakidae), coffin ray (*Hypnos monopterygius*, Hypnidae) and western shovelnose ray (*Aptychotrema vincentiana*, Trygonorrhinidae) (Table S7).

There is no exposure to demersal shark gillnets for the chondrichthyan species in the shelf-sand EG in the sub-region SNSW. A prohibition on shark gillnets in NSW has existed since their introduction to southern Australia's shark fishery in the late 1960s. However, historically the shelf-sand EG has received high demersal trawl fishing effort in SNSW. The state-managed Queensland East Coast Otter Trawl Fishery targets several species of prawns, the saucer scallop (*Ylistrum balloti*, Pectinidae), Balmain bug (*Ibacus peronii*, Scyllaridae) and stout whiting (*Sillago robusta*, Sillaginidae). Vessel number and vessel-fishing days in the 1990s fell to about two-thirds by 2001–2004 and below one-third by 2007–2014 in response to the *East Coast Trawl Management Plan 1999*. The reduction in fishing effort combined with by-catch reduction devices and adoption of square mesh in the codends for scallop trawl similarly reduced by-catch (Courtney et al., 2007; Wang et al., 2020). This fishery operating mainly on top of the continental shelf (maximum depth of 270 m) impacts only the shelf-sand ecological group. The Commonwealth-managed East Coast Deepwater Trawl Sector operates off southern Queensland and northern New South Wales, mostly south-east of Lord Howe Island (Georgeson & Curtotti, 2020). This mid-water trawl fishery targets the benthopelagic teleost alfonsino (*Beryx splendens*, Berycidae) but has a negligible impact on the bathyal-upper and bathyal-lower ecological groups.

Exposure to FO stressors in the study region and the entire Australian EEZ for the two past FO scenarios of 2000–2006 and 2018 relates to the distribution of fishing effort as indicated by available data and the areas of influence of 'other anthropogenic' stressors. However, evaluation of exposure to CC stressors according to alternative emissions scenarios requires a different approach. Envisaged CC scenarios defined by alternative projections of greenhouse gases in the atmosphere progress smoothly to the year 2100 (Table S4), whereas the loss of habitat or change in habitat suitability will be less predictably. Climate change has led to the emergence of large areas of waters with above long-term average temperatures ('hotspots') in south-western and south-eastern Australia and a series of marine heatwaves off southern Australia (Appendix S2). These changes have already produced ecological changes affecting the extent of habitats and their suitability for the chondrichthyan fauna. Although there may be some recovery of these habitats in the long term, further changing conditions and successive marine heatwaves will lead to a mosaic of variously modified habitats. While we assess exposure and vulnerability to CC stressors for emissions scenarios defined by radiative forcing and CO_2-eq concentrations in the year 2100, the effects of modified habitats on the population sizes of chondrichthyan species will occur well before 2100 Inevitably habitat modification will occur in parts of the study region after 2100. Thus, although emissions scenarios relate to 2100, for ESA–ESP analysis, vulnerability is the risk from climate change according to an envisaged emissions scenario rather than the abiotic and biotic conditions predicted for a specific year.

2.2.12 | Vulnerability of each species for 2 FO and 3 CC scenarios and their 6 combinations

Finally, for each species separately, we calculated the vulnerability of exposure to CC stressors, V_{CC}, for each of the three future CC scenarios (LE, ME and HE) given by

$$V_{CC} = \text{Exposure}_{CC} \times R_{CC},$$

the vulnerability of exposure to FO stressors, V_{FO}, for each of the two past FO scenarios (2000–2006 and 2018) given by

$$V_{FO} = \text{Exposure}_{FO} \times R_{FO},$$

and, following the formulation in Equation 1 for combining risks, the vulnerability of exposure to CC and FO stressors together, $V_{CC\,\&\,FO}$, for each of the six possible CC and FO combined scenarios (LE & 2000–2006, ME & 2000–2006, HE & 2000–2006, LE & 2018, ME 2018, HE & 2018) is given by

$$V_{CC\,\&\,FO} = 1 - \left(1 - V_{CC}\right)\left(1 - V_{FO}\right). \quad (3)$$

2.3 | Tailoring ESA–ESP analysis to other taxa and regions of the world

Before embarking on the 12 steps of ESA–ESP analysis, it is necessary to decide on the boundaries of one or more study regions; and perhaps, as in our study for assessing past fishing scenarios, enclosed within a broader region of jurisdiction or interest. We designed our study to inform conservation and resource management agencies of each chondrichthyan species with ≥20% of its present spatial distribution inside the southern region of the EEZ of Australia of its vulnerability to anthropogenic stressors. Species of <20%

need assessing in one or more separate study regions. As explained, each species' regionality is its spatial proportion of the species' distribution inside the Australian EEZ exposed to the FO stressors. The determination of risk to species with distributions extending to broader regions such as Australasia, the Southern Hemisphere or the world would require adjusting their regionality values to the broader region. Also, exposure values will likely require adjustment to the broader region.

Of the 132 species we assess, 57 have part of their distribution extending beyond the Australian EEZ. Our estimates of resilience risks for each species apply in any other region of the world where it occurs unless there are different FO stressors. However, a species' vulnerability will depend on its exposure to the stressors associated with the hazards of one or more specified anthropogenic scenarios.

For other parts of the world, such as the Mediterranean Sea and North Atlantic, where there are numerous independent jurisdictions managing fish stocks, there may be advantages assessing vulnerability for separate regions, as well as for two or more regions combined. An unpublished vulnerability analysis of the chondrichthyan fauna in the EEZ of western Mexico required a spatial approach because of the highly complex oceanographic conditions in some of those waters. The confluence of the equatorward-flowing cold water California Current and poleward-flowing warm water Mexican Coastal Current occurs at the Gulf of California entrance. The Gulf's large size, elongate shape, and stepping depth from <200 m at the head to >3,000 m at the entrance, low dissolved oxygen at depths >75 m, upwelling system, and high turbulence at the entrance required dividing the EEZ into three contiguous regions (inside the Gulf, the Gulf's turbulent entrance region and outside the Gulf in Mexico's Pacific waters) for separate analyses.

Some ESA–ESP analysis steps will require modification if applied to r-selected species (notably teleosts and invertebrates). Because many of these species might be distributed predominantly inshore, simply applying the precautionary principle for 'other anthropogenic' stressors, as in our study, would significantly reduce the variation in vulnerability estimates and thus the value of the analysis. One approach is to undertake the analysis applying the precautionary principle to 'other anthropogenic' stressors in the analysis and then, for those species at high or medium risk, repeat the analysis for climate change and fishing stressors without the 'other anthropogenic' stressors. That approach would allow identifying species potentially at increased risk from exposure to 'other anthropogenic' stressors, thus requiring investigation directed for improved information. For example, an investigation might include determining differences in the toxicity of specific chemicals released into the environment. Measures of encounterability and selectivity related to toxins' distribution may be feasible for ESA–ESP application. An alternative approach is to adapt sensitivity analyses of alterations in the distribution and abundance of marine species and the timing of their life-history events (phenology) as applied in other studies (Pecl et al., 2014).

We chose to simplify our ESA–ESP analysis application by grouping all these stressors as part of a single type of fishing inshore with maximum risk consistent with the precautionary principle. However, improvement of the analysis to include any single or mix of hazards explicitly is achievable by expanding Equations 2 and 3 using the formulation.

$$\text{Total risk} = 1 - \prod_{k=1}^{K} (1 - p_k)$$

where total risk is resilience risk or vulnerability, K is the number of hazards evaluated, and p_k is the risk contributed by the kth hazard. For example, $K = 3$ for analysis including the fishing, climate change and 'other anthropogenic' hazards, or $K = 4$ for analysis including, the fishing, climate change, chemical contamination and noise hazards. For 'other anthropogenic' stressors, the risk of a marked population reduction can relate to either changed mortality or changed habitat extent or suitability; however, when determining vulnerability, changed anthropogenic mortality or changed habitat needs relating to one or more scenarios of 'other anthropogenic' stressors. Because total risk approaches one as K increases, there are advantages in grouping all 'other anthropogenic' hazards as a single hazard or treating them as a single fishing type, as in our study.

It is feasible for other studies to apply our base case methods for determining risk for each risk factor, with the one exception of productivity risk. Given Z_{MSY} estimates become increasingly uncertain with decreasing maximum age, we suggest setting productivity risk at a minimum of 0.333 if a species' maximum age is less than 8 years or calculating productivity risk by interpolation over the maximum age, a_{max}, range 0–8 years using the linear equation where

$$\text{Productivity risk} = 0.0428\, a_{max}.$$

3 | RESULTS

We present resilience risk analysis results for 132 species of Chondrichthyes and exposure analysis for the two past observed FO scenarios (2000–2006 and 2018) with assumed zero CC stressors and three hypothetical future CC scenarios with assumed zero FO stressors. In addition, the vulnerability analysis results are for the two past FO scenarios, three hypothetical future CC scenarios and six hypothetical future CC-FO scenario combinations. For future CC-FO scenarios, each of the two past FO scenarios is assumed to continue through the present century. We avoid giving results for the whole EEZ for scenarios involving future scenarios because of the changing regionality (and thus susceptibility) of many of the species assessed. Hence, the results for future scenarios apply to only the study region of southern Australia, and results of species' exposure and vulnerability to FO stressors analyses in the entire Australian EEZ are presented for just the two past FO scenarios.

3.1 | Species assessed for risk

Of 132 chondrichthyan species (Table S3) identified as having ≥20% of their present Australian distribution area inside our study region, 35 species (26%) have their distribution wholly enclosed within the study region, 55 (42%) have ≥⅔ and <1 of their distribution inside, 30 (23%) have ≥⅓ and <⅔ inside, and 12 (9%) have <⅓ inside the study region. Overall, ~74% of their combined distributions are inside the study region and 26% outside in the remainder of the Australian EEZ.

The number of species varies widely among the ecological groups (EGs). The shelf-inshore EG (1 species, 1%) is the only group with 100% of its species' distribution inside the study region. Four of the other EGs have most of their species' Australian distributions inside the study region: shelf-reef (12 species, 9%) (with 59% of their combined distribution inside), shelf-sand (57, 43%) (76% inside), bathyal-upper (19, 14%) (72%) and bathyal-lower (39, 30%) (79%). The pelagic group (4, 3%) (40%) is the only EG with most of their combined distribution of its species outside (Table S3).

Taxonomically there are 37 squalomorph sharks (28% of the 132 species), 40 galeomorph sharks (30%), 45 rays (34%) and 10 chimaeras (8%). Concerning lifestyle, the number of demersal species on the continental shelf (70 species, 53%) (with 74% of their combined distributions inside the study region) exceeds the number on the continental slope (58, 44%) (77%), and that of demersal species (128, 97%) (74%) greatly exceeds pelagic species (4, 3%) (40%). The Australian distributions of the 4 pelagic species are negligible compared with their global distributions.

3.2 | Resilience risk of species to CC, FO, and combined stressors

Resilience analysis indicates that patterns in the resilience risks determined from species' attributes (Table S8) relate to the species' ecological groups, fishing types, taxonomic groups and bathymetric distributions. In general, adaptability and productivity risks are higher than the sensitivity and susceptibility risks (Figure 2a, b). High adaptability risk and high productivity risk, respectively, is consistent with the tendency for chondrichthyans to be high in food webs and long-lived compared with teleost and invertebrate species.

The pattern of percentages of the 132 species at H, M and L resilience risk in the study region vary among the four resilience components of adaptability (86%, 10% and 4%, respectively), productivity (79%, 21% and 0%), sensitivity (40%, 3% and 57%) and susceptibility (55%, 1% and 44%). High risk for adaptability and productivity occurs for species in all EGs, except for the shelf-inshore EG with its one species. This species—the maugean skate (*Zearaja maugeana*, Rajidae)—is H risk for adaptability and M risk for productivity.

The pattern of percentages of the 132 species in the three categories of risk (H, M and L) indicates that resilience risk is highest for FO and CC stressors combined (69%, 18% and 13%, respectively), followed by FO stressors (55%, 3% and 42%) and CC

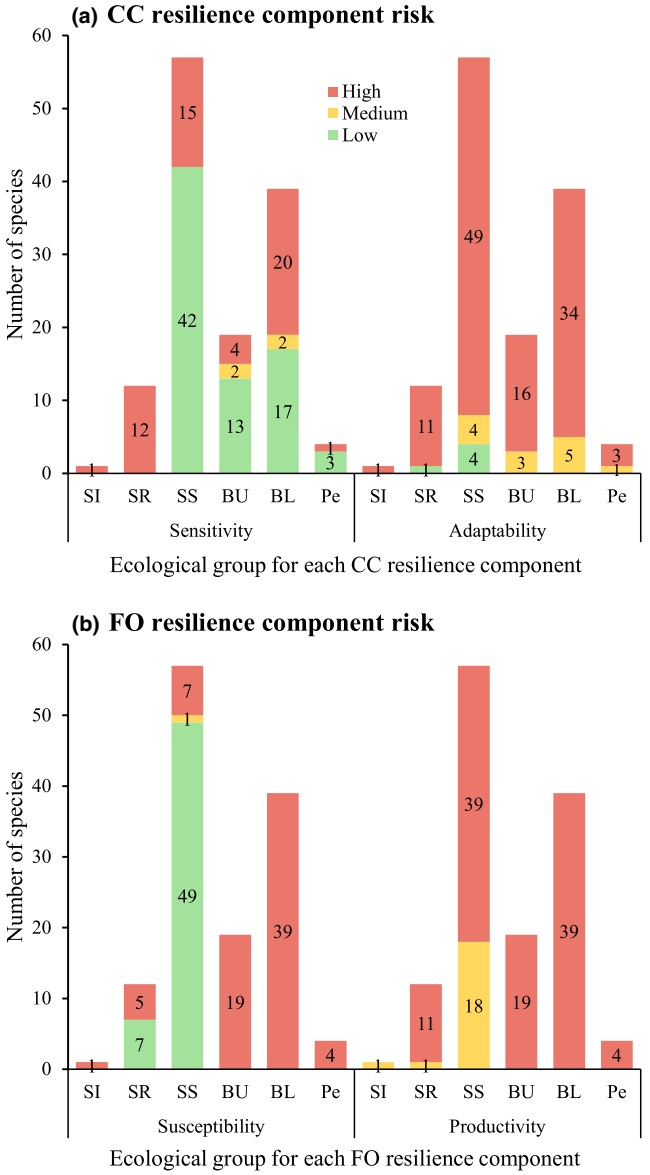

FIGURE 2 Number of species at high, medium or low resilience risk for each resilience component by ecological group (EG) to climate change (CC) (a) and fishing and 'other anthropogenic' (FO) (b) anthropogenic stressors. Ecological group: SI, shelf-inshore; SR, shelf-reef; SS, Shelf-sand; BU, bathyal-upper; BL, bathyal-lower; Pe, pelagic

stressors (37%, 5% and 58%). The resilience risk of the maugean skate, distributed inshore in estuarine waters (Awruch et al., 2021), the only species entirely within the range of non-industrial fishing and 'other anthropogenic' stressors, is H for CC and FO stressors combined, H for CC stressors and M for FO stressors (Figure 3a, b). Of the 57 species in the shelf-sand EG, the pattern of percentages indicates that resilience risk is highest for CC and FO stressors combined (30%, 40% and 30%), followed by CC stressors (24%, 2% and 74%), and then FO stressors (principally demersal shark gillnets) (9%, 5% and 86%). The pattern for the 12 shelf-reef species and 4 pelagic species, potentially available to hook fishing, follows the same order of resilience risk as the shelf-sand species

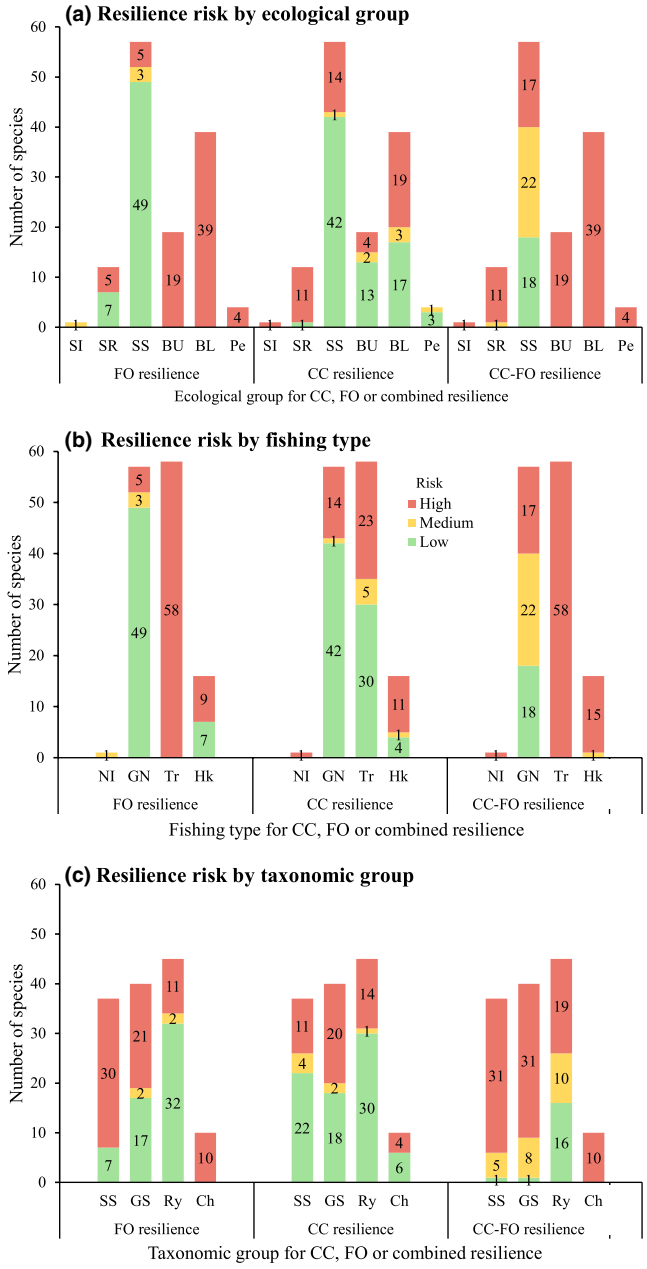

FIGURE 3 Number of species at high, medium, or low resilience risk by ecological group (a), fishing type (b) and taxonomic group (c) to climate change (CC), fishing and 'other anthropogenic' (FO) and combined CC-FO anthropogenic stressors. Ecological group: SI, shelf-inshore; SR, shelf-reef; SS, Shelf-sand; BU, bathyal-upper; BL, bathyal-lower; Pe, pelagic. Fishing type: NI, non-industrial; GN, demersal shark gillnet (150–165 mm mesh size); Tr, demersal trawl; Hk, hook. Taxonomic group: SS, squalomorph sharks; GS, galeomorph sharks; Ry, rays; Ch, chimaeras

distributed on the continental shelf for stressors of FO and CC combined (94%, 6% and 0%), CC (69%, 6% and 25%) and FO (56%, 0% and 44%). The 58 species distributed on the continental slope (i.e., bathyal-upper and bathyal-lower EGs) are at higher resilience risk to demersal trawl than are the species on the shelf to demersal shark gillnet and hooks. The patterns for the species on the slope is highest resilience risk for CC and FO stressors combined (100%, 0% and 0%), followed by FO stressors (100%, 0% and 0%), and then CC (40%, 8% and 52%).

The pattern of percentages of the 132 species in the three risk categories indicates that resilience risk to FO stressors among the four taxonomic groups (Figure 3c) follow the order from highest to lowest risk of chimaeras (100%, 0% and 0%), squalomorph sharks (81%, 0% and 19%), galeomorph sharks (52%, 5% and 43%) and rays (25%, 4% and 71%). For CC stressors, the order of these taxa changes to galeomorph sharks (50%, 5% and 45%), chimaeras (40%, 0% 60%), squalomorph sharks (30%, 11% and 59%) and rays (31%, 2% and 67%). The order for FO and CC stressors combined is the same as for FO stressors of chimaeras (100%, 0% and 0%), squalomorph sharks (84%, 16% and 0%), galeomorph sharks (78%, 20% and 2%) and rays (42%, 22% and 36%).

The taxonomic groups' bathymetric distribution patterns largely explain their differences in resilience to human-induced stressors. Distributed mostly on the continental slope, squalomorph sharks (78%) and chimaeras (90%) have high susceptibility risk to demersal trawl and low resilience risk to CC stressors. Conversely, galeomorph sharks (78%) and rays (76%), distributed mainly on the continental shelf, mostly have low susceptibility risk to highly length-selective demersal shark gillnets and high resilience risk to CC stressors.

3.3 | Exposure of each EG to CC and FO stressors by scenario

The exposure to CC stressors for chondrichthyan species is highest in inshore and surface waters and declines progressively with increasing depth, particularly in the uppermost 75 m. At depths ≥200 m (i.e., 76% of the area of the study region), exposure of the bathyal-upper and bathyal-lower EGs is scored low for the low (LE), medium (ME) and high emissions (HE) scenarios. As discussed below, ongoing ocean acidification will eventually increase chondrichthyans' vulnerability, but we assume their resistance during our analysis timeframe of the present century. The Flinders current and upwelling will continue cooling habitats within the bathymetric range of the bathyal-upper EG and much of the area on the continental shelf, particularly the outer parts at depths >75 m (i.e., 37% of the shelf area and 9% of the area of the study region). We expect the exposure of the remaining four EGs (shelf-inshore, shelf-reef, shelf-sand and pelagic EGs) to CC stressors to vary depending on the emissions scenario (Tables 3a, b).

The shelf-inshore EG in shallow waters will experience M or H exposure to rapidly changing habitats resulting from rising water temperature, sea level, storm impacts and UV light radiation for all three emissions scenarios. The species in the pelagic EG distributed throughout the study region will experience increased water temperature. However, pelagic species have the flexibility to descend to colder water or move south towards the cold Antarctic Circumpolar Current or other cooler regions outside Australia's EEZ, such as off south-eastern New Zealand. More uncertain is the exposure of the shelf-reef and shelf-sand EGs because the species of these EGs might

TABLE 3A Exposure of each ecological group of chondrichthyan species to stressors associated with 'other anthropogenic' hazards

Anthropogenic stressor	Description of stressors contributed by 'other anthropogenic' hazards	Exposure of each ecological group					
		SI	SR	SS	BU	BL	Pe
Environmental modification	Substrate disturbance by fishing, discarded and lost fishing gear, land reclamation, retaining walls, piers, pylons, oil and gas platforms and pipelines, wind and tidal turbines, channel deepening and beach renourishment altering geomorphology, hydrology and biochemical processes. These impact on chondrichthyan habitats, including food availability and nursery areas.	H	L	L	L	L	L
Artificial electric and electromagnetic fields underwater	Electrolysis from metal pylons, walls, oil and gas platforms and pipelines, wind and tidal turbines, and electromagnetic fields from direct current high voltage and telecommunication cables affecting chondrichthyan sensory electroreception used for prey, predator, and mate detection and migration (Walker, 2001).	H	L	L	N	N	N
Artificial noise underwater	Noise from shipping, boating, structural works, and seismic survey for mineral, oil and gas exploration affecting chondrichthyan sensory mechanoreception (McCauley et al., 2017) used for prey, predator, and mate detection and migration.	H	L	L	L	L	L
Artificial light underwater	Light from shipping, boating and structural works stimulating chondrichthyan sensory photoreception used for prey, predator, and mate detection and migration.	H	L	L	L	L	L
Hydrocarbon, microplastics, and other chemical contamination	Hydrocarbon and other chemicals from shipping oil-spills and bilge pumping, oil and gas field installation leaks, industrial discharges, sewage outfalls, urban stormwater and agricultural run-off, and ocean dumping of ores and other materials contaminating chondrichthyan body tissues affecting sensory chemoreception used for prey, predator, and mate detection and migration. Most oil and gas production in the region is from the Gippsland Basin off eastern Victoria and Otway Basin off western Victoria, with exploration undertaken or proposed in the Great Australian Bight and the Sorell Basin off west Tasmania.	H	L	L	L	L	L
Nutrient enrichment	Nutrients from sewage outfalls, urban stormwater, agricultural run-off and fish farming altering chondrichthyan habitats, food availability and frequency of hypoxia.	H	L	L	N	N	N
Invasive species	Invasive species from shipping altering chondrichthyan habitats and food availability.	H	L	L	L	L	L

Note: Ecological group: SI, shelf-inshore; SR, shelf-reef; SS, Shelf-sand; BU, bathyal-upper; BL, bathyal-lower; Pe, pelagic. Exposure: N, nil or negligible; L, low; M, medium; H, high risk.

move to deeper water on the outer parts of the continental shelf or upper slope to reduce exposure to CC stressors. Hard substrate habitat required by species of the shelf-reef EG occurs at most depths <200 m. Although precise estimates of hard substrates by bathymetric depth are not available, distribution of the southern rock lobster total catch from this habitat adjacent to Victoria indicates that most of the reef habitat is in the shallower parts of the continental shelf. The catch was 56% from depths of <40 m, 28% from 40–79 m and 16% from ≥80 m during the 34 annual fishing seasons beginning in November 1978 (Walker et al., 2013). We acknowledge that fuel costs, traveling time and poor weather conditions deter more distant deep-sea fishing and underestimate the extent of deep reef habitat, but consider the method to provide a reasonable guide. Furthermore, the inshore reefs are likely more productive and thus have higher rock lobster densities. On the other hand, reef productivity would presumably affect the shelf-reef chondrichthyans in the same way.

Because most of the area occupied by the shelf-reef EG is <75 m, exposure of this EG and its habitats to rising water temperatures will increase as emissions rise. Species in the shelf-sand EG inhabiting these depths also face rising water temperatures but have greater flexibility. These species can move deeper towards the outer edge of the continental shelf or westwards away from the influence of the East Australian Current to the cooler central parts of the continental shelf of southern Australia (Appendix S1). Maps of the projected average change in monthly SST based on nine models in the OzClim suite in the year 2050 show that the slowest rate of warming is off South Australia and western Victoria (Hobday & Lough, 2011). Although species of the shelf-sand EG, and to a lesser degree those of the shelf-reef EG, may have the flexibility to move to the deeper water, redistribution will not favour all species equally. Species presently inhabiting the shelf's outer parts will have advantages over those inhabiting inner parts given differences in the food chains and

TABLE 3B Exposure of each ecological group to stressors for three future climate change emissions scenarios and two past fishing and 'other anthropogenic' scenarios

Anthropogenic stressor	Description of stressors associated with anthropogenic hazards	Anthropogenic scenario	Exposure of each ecological group					
			SI	SR	SS	BU	BL	Pe
Climate change hazard								
Climate change stressors	Rising water temperature (particularly the surface 75 m), rising sea level, changing rainfall and freshwater run-off, increasing storm frequency and intensity, changing currents and upwelling, increasing UV light radiation, decreasing dissolved oxygen concentration, and increasing ocean acidity.	CC LE	M	L	L	L	L	L
		CC ME	H	M	L	L	L	M
		CC HE	H	M	M	L	L	M
Fishing and 'other anthropogenic' hazards								
Non-industrial demersal inshore fishing type together with 'other anthropogenic' stressors	Recreational use of rod and reel and artisanal use of hooks, gillnets and seine nets from small boats and shore causes fishing mortality to chondrichthyan species as target catch, by-product and by-catch. This fishing occurs at high intensity in gulfs, bays, inlets, and estuaries and less intensity in coastal ocean waters. 'Other anthropogenic' stressors (Table 3a) add to fishing mortality in these localities. Most 'other anthropogenic' stressors are inshore, but isolated hydrocarbon extraction, seismic survey (McCauley et al., 2017) and high-voltage direct current cables (Walker 2001) occur mainly offshore on sandy substrates.	FO 2000–06	H	L	L	L	L	L
		FO 2018	H	L	L	L	L	L
Industrial demersal trawl fishing type	Industrial demersal trawl cause fishing mortality to chondrichthyan species as target catch, by-product and by-catch from high fishing effort over most of the upper continental slope areas and moderate fishing intensity in some parts on the continental shelf, but prohibited in the bays, inlets and estuaries, and since 2007 on the continental slope at depths greater than 700 m. Fishers avoid rocky and other hard substrates to minimize damage to the fishing equipment.	FO 2000–06	L	L	MH	H	H	L
		FO 2018	L	L	MM	M	L	L
Industrial demersal shark gillnet (150–165 mm mesh size) fishing type	Industrial demersal shark gillnets cause fishing mortality to chondrichthyan species as target catch, by-product and by-catch from high fishing effort over large areas on the continental shelf at depths mostly <75 m. Gillnets target gummy sharks but are prohibited in bays, inlets, estuaries, inside 3 NM of the Victorian coast, and large areas off South Australia. Fishers avoid rocky and other hard substrates to minimize damage to the fishing equipment. Gillnets are highly length-selective depending on the size and body shape of the animal (Figure S1).	FO 2000–2006	L	L	HN	L	L	L
		FO 2018	L	L	MN	L	L	L
Industrial demersal longline fishing type†	Industrial demersal longlines with baited hooks cause fishing mortality to chondrichthyan species as target catch, by-product and by-catch from low fishing effort on parts of the continental shelf and continental slope in the past. Longlines were phasing out, but there is potential for their re-introduction following the closure of large coastal areas off South Australia to gillnets to protect sea lions.	FO 2000–2006	L	L	L	L	L	L
		FO 2018	L	L	L	L	L	L

(Continues)

TABLE 3B (Continued)

Anthropogenic stressor	Description of stressors associated with anthropogenic hazards	Anthropogenic scenario	Exposure of each ecological group					
			SI	SR	SS	BU	BL	Pe
Industrial and game pelagic fishing type	Industrial pelagic fishing using hook, jig and purse seine in the uppermost 200 m causes fishing mortality to chondrichthyan species as target catch, by-product and by-catch from low fishing effort over the EEZ of southern Australia concentrated in specific areas targeting squid, tunas and clupeoids. Game fishers using rod and reel to target mostly shortfin mako but catch porbeagle, blue shark and small amounts of other species.	FO 2000–2006	L	L	L	L	L	L
		FO 2018	L	L	L	L	L	L

Note: Ecological group: SI, shelf-inshore; SR, shelf-reef; SS, Shelf-sand; BU, bathyal-upper; BL, bathyal-lower; Pe, pelagic. Climate change (CC) scenarios: LE, low emissions; ME, medium emissions; HE, high emissions (Table S4). Fishing and 'other anthropogenic' (FO) scenarios: FO 2000–06; FO 2018. Exposure: N, nil; L, low; M, medium; H high based on the proportion of the distributional area of an ecological group exposed to a fishing type. Exposure to industrial demersal shark gillnet and industrial demersal trawl for species in the shelf-sand ecological group separates westwards (43 species distributed mainly off Australian south coast and sub-region NW) and eastwards (14 species distributed mainly in the sub-regions of NE and SNSW), respectively. See Figure 1 for sub-regions.

†For the sand-shelf ecological group, industrial demersal longline is subsumed by industrial demersal trawl in sub-regions NE and SNSW and industrial shark gillnet in the other sub-regions. For the shelf-upper and shelf-lower ecological groups, industrial demersal longline is subsumed by industrial demersal trawl in all sub-regions.

overall ecological productivity among the various continental shelf parts.

Exposure to fishing declined from the period 2000–2006 to the year 2018 following the closure of depths ≥700 m to most fishing, the closures of large areas of waters on the continental shelf off South Australia from shark gillnet fishing to protect sea lions, and a contraction of the area fished with the halving of fishing effort. These fishery management actions reduced exposure to industrial demersal shark gillnet fishing from H to M for the shelf-sand EG. Furthermore, these actions reduced exposure to industrial demersal trawl from H to M for the bathyal-upper EG and H to L for the bathyal-lower EG. Exposure to non-industrial inshore fisheries, combined with 'other anthropogenic' stressors, remains H for the shelf-inshore EG. Offshore, however, the 'other anthropogenic' stressors occur only briefly or in small proportions of the area occupied by each of the EGs; thus, exposure was N or L (Table 3a). Exposure to demersal trawl remained unchanged at M for the shelf-sand EG; otherwise, exposure was L for all other EGs and other types of fishing. As an input to calculating vulnerability, for the CC and FO stressors, we set the overall exposure of each EG to the exposure of the stressors exhibiting the highest exposure value (Table 3b, Figure 4a, b).

Exposure analysis showed that for the CC LE scenario without FO stressors, all species are at L exposure to CC stressors, other than the one species, the maugean skate in the shelf-inshore EG, which is at M exposure (Table S9, Figure 4a). Exposure of the shelf-inshore EG would increase to H and the pelagic EG to M for the more severe CC ME and CC HE scenarios. In contrast, the shelf-reef EG exposure would increase to M and H for the CC ME and HE scenarios, respectively. Only the two EGs on the continental slope (bathyal-upper and bathyal-lower) would remain at L exposure for all three CC-only scenarios through the present century.

Because 29 of the 37 species of squalomorph sharks (78%) and 9 of the 10 species of chimaeras (90%) occur on the continental slope in deep water, these taxonomic groups would experience L exposure to CC stressors for the three CC only scenarios (Figure 4c). On the other hand, 31 of the 40 species of galeomorph sharks (78%) and 34 of the 45 rays (76%) occur in shallower waters on the continental shelf or in pelagic waters, and these taxonomic groups would experience progressively higher exposure with increasing severity of the CC scenario. The only taxonomic groups to experience H exposure would be the galeomorph sharks (9 species equivalent to 23%) for the CC HE scenario and the ray species for the CC ME scenario (1 species, 2%) and CC HE scenario (4 species, 9%). All groups would variously experience M exposure for one or more of the CC scenarios. All species of the four taxonomic groups were at H exposure to FO stressors for the FO 2000–2006 scenario except for 16 species (13 galeomorph sharks and 3 rays) in the shelf-reef and pelagic EGs at L exposure to hook fishing. Reduced shark gillnetting and demersal trawl from the FO 2000–2006 to the FO 2018 scenario reduced exposure to L or M for the squalomorph sharks (54% and 46% of species, respectively), galeomorph sharks (47% and 53%), rays (20%

and 78%) and chimaeras (70% and 30%). Only the one ray species, the maugean skate, remained at H exposure in 2018.

3.4 | Vulnerability of species to each CC, FO and combined CC-FO scenario

Vulnerability analysis indicates that the risk of a marked population decline varied widely among the 132 chondrichthyan species depending on EG, fishing type, taxonomic group and anthropogenic scenario (CC, FO or combined CC-FO) (Figure 5, Table S9, S10). For some of those species with part of their distributions extending north of the study region, the vulnerability category (H, M or L) differed between the study region and the entire Australian EEZ, depending on their regionality and their EG's exposure level.

For the shelf-sand EG, combining the NW and NE sub-regions with the study region to cover all of that part of the EEZ at H or M exposure to demersal shark gillnetting and demersal trawling increases the combined species distribution from 76% inside the study region to 99% of the expanded region. For all EGs, the distribution of the 132 species combined exposed to FO stressors increases from 74% inside the study region to 84% inside the expanded region. The remaining 16% of the combined distribution falls outside the expanded region in the Australian EEZ, free of H or M exposure to the FO stressors.

For the two past FO scenarios (FO 2000–2006 and FO 2018), the pattern of the number of species at H, M or L vulnerability for the EEZ (Figure 6) was the same as for the study region in the shelf-inshore, shelf-reef and pelagic EGs (Figure 5a), because of L exposure in both the study region and entire EEZ. For the shelf-sand EG, although the exposure was H (east coast from trawl) or *M* (south and west coasts from demersal shark gillnets), there was no difference in vulnerability between the study region and the whole EEZ because the exposure categories were the same in both regions. However, for some species in the bathyal-upper and bathyal-lower EGs, differences in vulnerability occurred between the two regions due to H or M exposure in the study region but L exposure to the north. Over the 132 species, the pattern of numbers at H, M and L risk shows that vulnerability in the study region for the scenarios FO 2000–2006 (48%, 3% and 49%, respectively) and FO 2018 (0%, 20% and 80%) was considerably higher than in the whole EEZ for the scenarios FO 2000–2006 (28%, 20% and 52%) and FO 2018 (0%, 17% and 83%). The differences between the periods and regions demonstrate the benefits of limiting exposure and having refugia to reduce vulnerability.

Inside the study region in the absence of FO stressors, over the 132 species, the patterns of the proportions in the three categories of vulnerability (H, M or L) indicate rising risk with the severity of the CC emissions scenario: CC LE (0%, 1% and 99%, respectively), CC ME (1%, 8% and 91%) and CC HE (9%, 11% and 80%). For the CC LE scenario, the vulnerability would be L for all species, except for the maugean skate at M risk (Figure 5a). The risk to this skate in the shelf-inshore EG would increase to H under the CC ME and CC HE scenarios. Of the 12 species

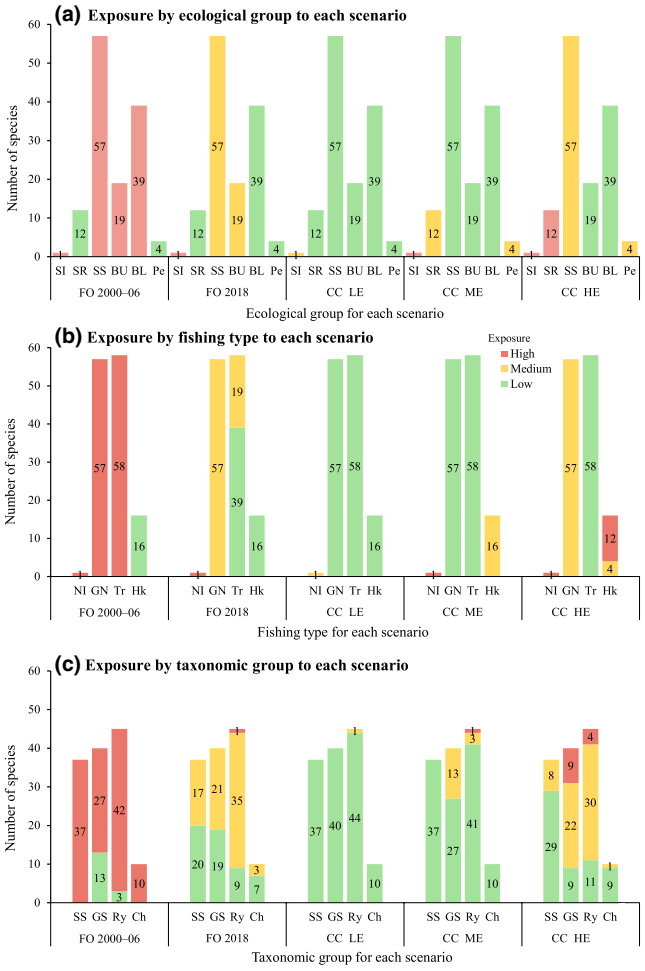

FIGURE 4 Number of species at high, medium or low exposure by ecological group (a), fishing type (b) and taxonomic group (c) to the anthropogenic stressors of each CC and FO scenario in the study region. Climate change (CC) scenario: LE, low emissions; ME, medium emissions; HE, high emissions. Fishing and 'other anthropogenic' (FO) scenario: FO 2000–2006; FO 2018. Ecological group: SI, shelf-inshore; SR, shelf-reef; SS, Shelf-sand; BU, bathyal-upper; BL, bathyal-lower; Pe, pelagic. Fishing type: NI, non-industrial; GN, shark gillnet (150–165 mm mesh size); Tr, demersal trawl; Hk, hook. Taxonomic group: SS, squalomorph sharks; GS, galeomorph sharks; Ry, rays; Ch, chimaeras

in the shelf-reef EG at L risk for the CC LE scenario, 11 (92%) would increase to M risk for the CC ME scenario and H risk for the CC HE scenario. Of the 57 species in the shelf-sand EG, which would all be at L risk for the CC LE and ME scenarios, 15 (26%) would be at M risk for the CC HE scenario. The numbers of shelf-sand species at H, M or L vulnerability from FO stressors (predominantly demersal shark gillnet) in the absence of CC stressors was higher for the FO 2000–2006 scenario (9%, 5% and 86%, respectively) than the FO 2018 scenario (0%, 12% and 88%) (Figure 5a, b).

In the study region, although the vulnerability of the 58 species distributed on the continental slope would be L for all three CC emissions scenarios, all of these species were at H risk from exposure to FO stressors (predominantly demersal trawl) during 2000–2006. By 2018, the risk levels dropped to M for the 19 bathyal-upper species

and L for the 39 bathyal-lower species. On the other hand, over the entire Australian EEZ, of the 19 bathyal-upper species in the proportions at H, M or L vulnerability during 2000–2006 (i.e., 42%, 42% and 16%, respectively) fell by 2018 (0%, 74% and 26%). A more significant vulnerability fall occurred for the 39 bathyal-lower species from 2000–2006 (49%, 49% and 2%) to 2018 (0%, 0% and 100%) in response to closing waters ≥700 m deep.

Except for the shelf-reef and pelagic EGs, the similarity between the patterns of FO resilience risk (Figure 3a–c) and vulnerability (Figure 5a–c) for the FO 2000–2006 scenario is consistent with most of the chondrichthyan fauna in the study region being close to maximum exposure to FO stressors during 2000–2006. This consistency indicates that ESA–ESP resilience analysis could have identified the most vulnerable species before 2000 by assuming H exposure to FO stressors. Although ESA–ESP analysis shows that many southern Australian chondrichthyan species are at H or M resilience risk to FO stressors, the CC scenarios are insufficiently severe to produce similar H or M vulnerability numbers. However, consistent with resilience risk analysis, the vulnerability of species exposed to CC and FO stressors together is higher than that from either only CC or only FO stressors (Figure 6). The patterns of the proportions of the 132 species at H, M and L vulnerability for the FO 2000–2006 scenario alone and the three CC scenarios combined with the FO 2000–2006 scenario indicate rising risks with climate change severity: FO 2000–2006 only (48%, 3% and 49%, respectively), CC LE & FO 2000–2006 (48%, 25% and 27%), CC ME FO 2000–2006 (54%, 21% and 25%) and CC HE & FO 2000–2006 (61%, 20% and 19%). Although the overall risks are lower, a similar pattern occurs for the FO 2018 scenario alone and the three CC scenarios combined with the FO 2018 scenario: FO 2018 only (0%, 20% and 80%), CC LE & FO 2018 (8%, 54% and 38%), CC ME & FO 2018 (13%, 51% and 36%) and CC HE & FO 2018 (19%, 53% and 28%).

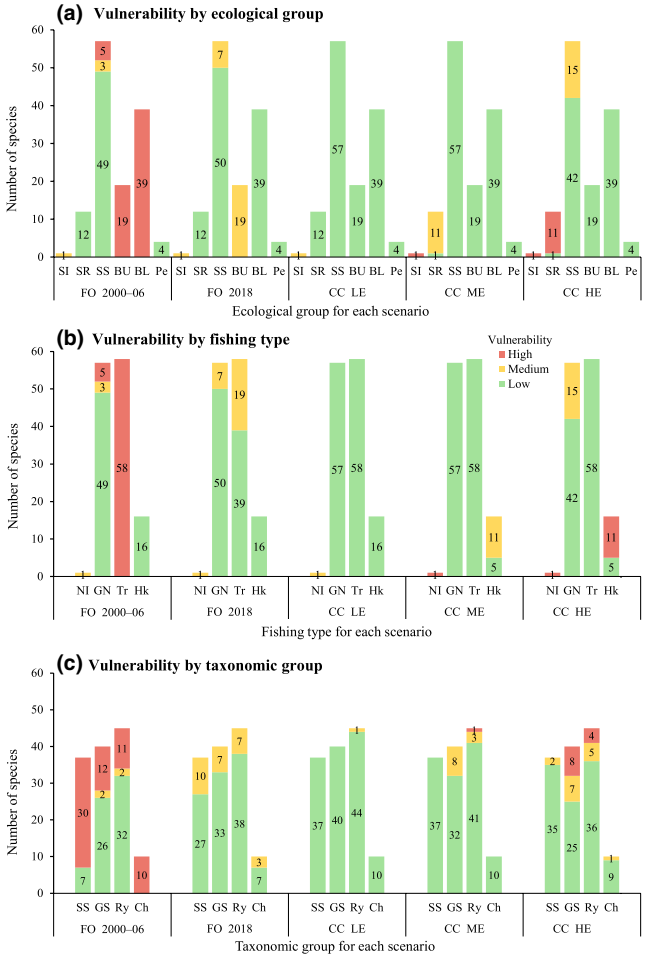

FIGURE 5 Number of species at high, medium or low vulnerability by ecological group (a), fishing type (b) and taxonomic group (c) to the anthropogenic stressors of each CC and FO scenario in the study region. Climate change (CC) scenario: LE, low emissions; ME, medium emissions; HE, high emissions. Fishing and 'other anthropogenic' (FO) scenario: FO 2000–2006; FO 2018. Ecological group: SI, shelf-inshore; SR, shelf-reef; SS, Shelf-sand; BU, bathyal-upper; BL, bathyal-lower; Pe, pelagic. Fishing type: NI, non-industrial; GN, shark gillnet (150–165 mm mesh size); Tr, demersal trawl; Hk, hook. Taxonomic group: SS, squalomorph sharks; GS, galeomorph sharks; Ry, rays; Ch, chimaeras

4 | DISCUSSION

4.1 | Robustness of ESA–ESP analysis

Testing the sensitivity of assigned and calculated risk determined from decision rules and varying the parameters of equations (Appendix S3; Table S6) on the total number of species at H or M vulnerability (Appendix S4; Table S11) indicate our results are reasonably robust. Our resilience risk estimates are comparable to those of other studies investigating the same species. In Appendix S4, we discuss the uncertainty associated with assumptions assigning risk to attributes as risk factors, the uncertainty in risk from simplifying assumptions underlying ESA–ESP analysis, and the implications of potentially unidentified risk factors. We also discuss the advantages of avoiding averaging productivity scores and adopting maximum age rather than reproductive metrics for scoring the productivity risk of chondrichthyans. There are also advantages in replacing the commonly adopted linear and additive relationship between productivity and susceptibility scores by treating productivity and susceptibility as independent risk factors, together with exposure, as multiplicative vulnerability components.

4.2 | Resilience of chondrichthyan species

During its long evolutionary history, life in Earth's oceans has experienced conditions far more extreme than those likely to be encountered during the remainder of the present century, for even the highest projected emissions scenarios (IPCC, 2013a). However, the survival of marine species during past periods of extreme conditions has varied widely among different taxonomic groups, and the recent and projected pace of change, particularly in the waters

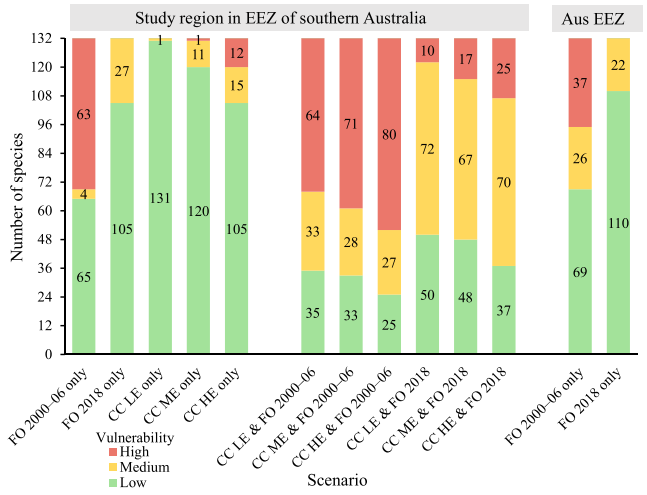

FIGURE 6 Number of species at high, medium or low vulnerability to the anthropogenic stressors of each CC, FO and CC-FO combined scenario in the study region and each FO scenario in the Australian EEZ. EEZ, Exclusive Economic Zone; Aus, Australian. Climate change (CC) scenario: LE, low emissions; ME, medium emissions; HE, high emissions. Fishing and 'other anthropogenic' (FO) scenario: FO 2000–06; FO 2018

of south-eastern Australia, far exceeds historical rates (Hobday & Lough, 2011).

The chondrichthyans survived better than the bony fishes and invertebrates during the mass extinction events at the ends of the Permian and Triassic following basalt eruptions (Vázquez & Clapham, 2017), leading to paleo-atmospheric CO_2 concentrations of ~3,000 ppm (Ekart et al., 1999), ocean warming, and reductions in pH and dissolved oxygen. Invertebrates undergo acidosis (decreased pH of body fluids) under elevated CO_2, but chondrichthyans and bony fishes have well-developed acid-base regulation via active ion exchange with buffering in the epithelial membranes of their gills (Claiborne et al., 2002). Marine fishes tend to be less resistant to hypoxia than invertebrates, but they are active organisms and have thermal tolerance scope. Globally over the past 200 years, the oceans have absorbed 30% of anthropogenic CO_2 emissions, which has decreased dissolved carbonate ions and pH by ~0.10 units (equivalent to a 26% increase in hydrogen ion concentration) (IPCC, 2013a). Reduced carbonate ion concentration has profound implications for marine organisms forming shells and skeletons, mostly of calcium carbonate in the form of calcite and aragonite. Affected invertebrates include corals, molluscs, arthropods, echinoderms, coccolithophores and foraminifera). Mineralization of cartilage in chondrichthyans and bone formation in other vertebrates require calcium phosphate in the form of hydroxyapatite, which is less sensitive to acidity (Ruben & Bennett, 1987).

Highly uncertain at present is the resilience and vulnerability of chondrichthyans to increasing chemicals, noise, light and electromagnetic fields underwater (i.e., 'other anthropogenic' stressors). Reduced sensory acuity from diminished chemoreception, electroreception, magnetoreception, mechanoreception or photoreception likely reduces competitiveness.

4.3 | Uncertainty of risks from CC stressors for chondrichthyan species

Of the eight CC stressors, we consider ocean acidification impacts pose the highest uncertainty for chondrichthyan species. Although paleontological information suggests chondrichthyan species are likely to be resilient to ocean acidity, recent experimental evidence suggests that the physiology, behaviour and survival of some species might be affected by high emissions scenarios through the remainder of the present century.

A review of experimental research on the biological impacts of acidification on a broad diversity of about 100 marine species indicates a wide range of species' responses (Kroeker et al., 2013). These responses include enhanced sensitivity of early life history stages of many but not all taxonomic groups, reduced calcification rates in molluscs, impaired homing ability in reef teleosts and increased macroalgae growth rates. Among chondrichthyan species, the foraging and shelter-seeking behaviours of juvenile epaulette sharks (*Hemiscyllium ocellatum*, Hemiscylliidae) were observed not to be affected by acidification of water exposed to atmospheric CO_2 concentrations simulating ME and HE scenarios (Heinrich et al., 2016). Furthermore, neither the resting metabolic rate nor hypoxia sensitivity of *H. ocellatum* was affected by long-term exposure to elevated CO_2 (Heinrich et al., 2014). Experiments on the eggs of the oviparous tropical brownbanded bamboo shark (*Chiloscyllium punctatum*, Hemiscylliidae) treated with temperature differences of 4°C, and pH differences of 0.5 units indicated a range of responses. Increased temperature, but not increased acidity, significantly reduced the survival rates and the period of embryogenesis, and increased yolk consumption, growth and metabolic rates of embryos (Rosa et al., 2018). A similar study of neonates of the closely related whitespotted bamboo shark (*Chiloscyllium plagiosum*, Hemiscylliidae) found resilience to a smaller pH difference of 0.3 units over 45 days in growth and behaviour tests. Newly hatched little skates (*Leucoraja erinacea*, Rajidae) following their exposure while in the egg to increased warming and acidification led to earlier exploration, feeding and potential exposure to predation (Di Santo, 2015). Port Jackson sharks (Pistevos et al., 2015) and dusky smoothhounds (*Mustelus canis*, Triakidae) (Dixson et al., 2015) exposed to elevated levels of CO_2 were slower and less successful finding prey through olfaction. Small-spotted catshark (*Scyliorhinus canicula*, Scyliorhinidae) exposed to elevated CO_2 buffered internal acidosis by increasing and maintaining the concentration of bicarbonate and sodium ions in the blood plasma (Green & Jutfelt, 2014). Some of these shark species also had various other physiological and behavioural responses to elevated CO_2. The short duration (several weeks or months) of these experiments under artificial and confined conditions are likely to have induced additional stressors. The experiments could not detect potential long-term adaptation to ocean acidity during the remainder of this century (Rosa et al., 2017), but they suggest possible effects. The pufferadder shyshark (*Haploblepharus edwardsii*, Scyliorhinidae) endemic to South Africa and experiences exposure each summer to 3–10-day cycles of hypercapnic water (pH 7.4–7.6)

and occasional extremes of pH 6.6 associated with upwelling of the Benguela Current. In response, this species physiologically adjusts its acid-base balance to acute and chronic hypercapnia. Prolonged exposure experimentally (9 weeks at a pH of 7.3), however, causes the dissolution of fluorapatite, leading to the corrosion and weakening of denticle surfaces. Impaired functionality of the denticles reduces fitness through affected hydrodynamics and skin protection with implications for feeding, predator avoidance and mating (Dziergwa et al., 2019).

In addition to the changed effects of climate change on primary production (Brown et al., 2010; Fulton, 2011), we acknowledge that future ocean acidification is potentially a CC stressor contributing directly to marked reductions in populations of chondrichthyan species in all the ecological groups we adopt. However, there will be a time lag as water acidified at the ocean's surface is gradually redistributed from the surface (mainly in cold water at the poles) into deeper water in all the oceans by oceanic circulation mixed into shallower depths by upwelling. Nevertheless, we account for chondrichthyan species' adaptability to increased ocean acidity in our ESA–ESP analysis by assuming changes in food chains where species at higher trophic levels are at higher risk of failing to adapt than those at lower levels.

Other CC stressors accounted for by trophic level risk include reduced dissolved oxygen and increased UV light radiation. As the ocean warms, reduced dissolved oxygen in the water may have adaptive disadvantages for large fish. The argument that the ratio of gill surface area to body mass decreases with body size (Cheung et al., 2013; Pauly, 2021; Pauly & Cheung, 2018) implies that chondrichthyans are likely to be disadvantaged more than teleosts and invertebrates, given chondrichthyans are among the largest animals in the marine environment. In southern Australia, the ratio of the number of chondrichthyan to teleost animals caught in highly size-selective gillnets increases linearly with mesh size from 0.34 for a 2-inch (51 mm) mesh size to 24.25 for a 9-inch (229 mm) mesh size (Walker et al., 2005). Certain 'other anthropogenic' stressors such as hydrocarbons, microplastics and other chemicals have the potential to disrupt food chains. Bioaccumulation and bioamplification lead to increasing contamination of animal tissues at the higher trophic levels.

4.4 | History and prognosis for chondrichthyan species in southern Australia

Catches of chondrichthyan species of southern Australia increased steadily with the growth of the industrial demersal trawl fishery originating in New South Wales during 1915 and the industrial demersal shark longline fishery in Victoria during the mid-1920s (Appendix S5). By the early 1970s, the shark longline fishery had converted to a demersal shark gillnet fishery, which, together with the trawl fishery, spread widely across southern Australia. By the mid-1980s, the demersal trawl fishery operated down the entire continental slope. Numerous chondrichthyan species were highly vulnerable to demersal trawl, gillnets and hooks when overall fishing effort peaked during 2000–2006. Our ESA–ESP analysis indicates that their vulnerability fell rapidly by 2018 in response to a decade of fishery management reform, reducing the catches, fishing effort and available fishing grounds.

In the short term, we expect some recovery of the populations; however, depending on the severity of greenhouse gas emissions, the number of species at medium or high vulnerability will steadily rise if fishing persists according to the 2018 fishing scenario (including current 'other anthropogenic' stressors). Vulnerability from the combined effects of climate change and fishing will inevitably vary among chondrichthyan species but rise overall in southern Australia. Many present species' distributions will contract westwards and maybe into deeper waters, particularly those distributed on the continental shelf over the broad sandy substrates. Furthermore, the Red List extinction risk classifications are unlikely to reduce for any of the five threatened species in southern Australia. As climate change exacerbates fishing risks, we expect the number of species at high or medium vulnerability and the number assessed with threatened status to rise off southern Australia and worldwide.

5 | CONCLUSIONS

1. The ESA–ESP analysis method for chondrichthyan species allows adequate assessment of the relative risks among species to any single or mix of anthropogenic stressors according to past, present or hypothetical future scenarios for determining mitigation, monitoring and research priorities. The assessments are fully transparent and repeatable.
2. When applied to chondrichthyan species, the method is readily adaptable to any region globally, but the procedures for calculating risk might require modification if used for taxa other than chondrichthyans, particularly short-lived species.
3. When applied to chondrichthyan species, the method is reasonably robust to our procedures for estimating risk but highly sensitive to dropping any of the adopted risk factors. The estimates of resilience risk and, thus, vulnerability are most sensitive to variation in values determined for the risk factors susceptibility, productivity and rarity.
4. Although estimates of resilience risk and vulnerability are affected by the method for determining productivity risk, there are sound arguments for calculating productivity risk as $1 - Z_{MSY}$, where Z_{MSY} is calculated directly from the maximum age observed for the species. However, this approach could be problematic for taxa, where the species are shorter-lived than our shortest-lived chondrichthyan species of 9 years, because of the biasing effects of fishing on the population's age structure.
5. In general, chondrichthyans have higher productivity risk and higher adaptability risk, thus higher resilience risk to anthropogenic stressors, than most teleost and invertebrate taxa in the marine environment.

6. Productivity risk is mainly H for squalomorph and galeomorph sharks and chimaeras but mixed evenly between M and H risk for rays for the 132 chondrichthyan species presently distributed predominantly off southern Australia.
7. Squalomorph sharks (78% of species) and chimaeras (90%) occur on the continental slope, where they have high susceptibility risk to demersal trawl but low resilience risk to CC stressors. Conversely, galeomorph sharks (78%) and rays (76%) occur on the continental shelf; they mostly have low susceptibility risk to highly length-selective demersal shark gillnets but have high resilience risk to CC stressors.
8. Risks of the marked reduction in population size fell between the period 2000–2006 when fishing effort peaked and the year 2018. A reduction in the number of species at H vulnerability to fishing from 63 to 0 inside our study region of southern Australia and from 37 to 0 inside the Australian EEZ was in response to the halving and contraction of demersal trawl and demersal shark gillnet fishing effort and the closure of most waters of depth ≥700 m and large areas of waters off South Australia to protect sea lions on the continental shelf.
9. Following reduced fishing effort by 2018, of the 27 species at M risk distributed on the shelf inshore (1 species), shelf offshore (7 species) and upper slope (19 species), most are now managed variously by either a prohibition on landing (4 species), a total allowable catch (4 species) or landing limits.
10. The difference in the number of species at H risk between our southern Australia study region and the entire Australian EEZ during 2000–2006 demonstrates the value of large refugia off Australia's west and east coasts, where demersal trawl on the continental slope is prohibited or has not developed.
11. In the longer term, if there were no fishing, 11 of 12 species dependent on reef habitats would be at M risk for climate change medium emissions and H risk for high emissions scenarios. Of those dependent on sandy substrates on the shelf, 15 of 57 species would be at M risk for high emissions scenarios. Species of particular concern in the not-so-distant future include the maugean skate with its full distribution inshore and 6 broadly distributed species. The six species are school shark, bronze whaler (*Carcharhinus brachyurus*, Carcharhinidae), dusky shark (*C. obscurus*), smooth hammerhead (*Sphyrna zygaena*, Sphyrnidae), broadnose sevengill shark (*Notorynchus cepedianus*, Hexanchidae) and elephant fish (*Callorhinchus milii*, Callorhinchidae) dependent on inshore nursery habitat. These 7 species are at H resilience risk from climate change and 'other anthropogenic' stressors inshore.
12. Overall, off southern Australia, susceptibility risk is much higher on the continental slope from demersal trawl (weakly size-selective) than on the continental shelf from demersal shark gillnets (highly size-selective). Gillnets are least effective at enmeshing small- and large-sized species, given their design to target mid-sized gummy sharks. However, offsetting the benefits of size selection by gillnets is a gradual increase in targeting gummy sharks with hooks increasing the species' mortality of breeding and pre-recruit animals. Reintroducing hook fishing will also increase the by-catch mortality of shortnose spurdog (*Squalus megalops*, Squalidae), whitespotted spurdog (*S. acanthias*), draughtboard shark, Port Jackson shark, broadnose sevengill shark and several ray species.
13. Off southern Australia on the continental slope, 29 squalomorph shark species (i.e., 78% of the 37 squalomorph species) and 9 chimaera species (90% of 10 species) have H susceptibility risk to predominantly demersal trawl and low resilience risk to climate change stressors. Conversely, on the continental shelf, 22 galeomorph shark species (55% of 40 species) and 32 ray species (71% of 45 species) have low susceptibility risk to mainly demersal shark gillnets and rising risks from climate change stressors. Although 4 pelagic species (all galeomorph shark species) have high resilience risk to hooks, historically, their exposure and vulnerability to hooks have been low.
14. As climate change progresses, depending on the level of emissions, tropical and subtropical species will further extend their distributional ranges into southern Australia and potentially displace some local species. This trend will be most pronounced in the shallower eastern parts on the continental shelf as the East Australian Current strengthens. The ranges of the present species on the continental shelf's southern parts are likely to contract westwards, with perhaps some shift to deeper water. Pelagic species can redistribute to colder regions of the ocean inside and outside the Australian EEZ, but the overall area of suitable conditions north of the Antarctic Circumpolar Current is likely to contract. All 58 species inhabiting the continental slope are at low vulnerability for all the climate change scenarios during the present century. However, risks will rise as acidifying water redistributes continuously from the poles to the continental slopes and shelves of all continents.
15. Climate change occurring together with fishing raises the number of species at higher risk. The challenge now for fisheries management is to develop fishing strategies to reduce the present species' fishing mortality through reduced fishing effort, improved by-catch reduction devices, and improved procedures for handling discarded animals. There may be a need to target specific species immigrating from the north.
16. Climate change occurring together with the present fishing scenario will cause at least six chondrichthyan species to remain threatened according to extinction risk criteria for the IUCN Red List. School shark, critically endangered; Harrison's dogfish (*Centrophorus harrissoni*, Centrophoridae) and maugean skate, endangered; and eastern angelshark (*Squatina albipunctata*, Squatinidae), grey nurse shark and sand tiger shark (*Odontaspis ferox*, Odontaspididae), vulnerable; will most likely require additional protection. Depending on the severity of future climate change, species currently not listed as threatened may eventually become threatened under the present fishing scenario.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The results are reproducible from the data, equations, algorithms and cited references presented in the present paper or supplementary figures and tables.

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[Correction added on 10 June 2021, after first online publication: The References have been amended in this version]

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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