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Conservation status of the Oyster Reef Ecosystem of Southern and Eastern Australia

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A B S T R A C T

Reef ecosystems all over the world are in decline and managers urgently need information that can assess management interventions and set national conservation targets. We assess the conservation status and risk of ecosystem collapse for the Oyster Reef Ecosystem of Southern and Eastern Australia, which comprises two community sub-types established by *Saccostrea glomerata* (Sydney rock oyster) and *Ostrea angasi* (Australian flat oyster), consistent with the IUCN Red List of Ecosystems risk assessment process. We established: (i) key aspects of the ecosystem including: ecological description, biological characteristics, condition and collapse thresholds, natural and threatening processes; (ii) previous and current extent of occurrence and current area of occupancy; and (iii) its likelihood of collapse within the next 50–100 years. The most severe risk rating occurred for Criterion A: Reduction in Extent (since 1750) and Criterion D: Disruption of biotic processes (since 1750), although assessment varied from Least Concern to Critically Endangered amongst the four criteria assessed. Our overall assessment ranks the risk of collapse for the ecosystem (including both community sub-types) as Critically Endangered with a high degree of confidence. Our results suggest the need for rapid intervention to protect remaining reefs and undertake restoration at suitable sites. Several restoration projects have already demonstrated this is feasible, and Australia is well equipped with government policies and regulatory mechanisms to support the future conservation and recovery of temperate oyster ecosystems.

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1. Introduction

Shellfish reef ecosystems develop when high densities of shellfish, typically oysters or mussels, occur and form biogenic structures that function as ecosystem engineers and the foundation of the ecosystem. Shellfish reef ecosystems support important environmental characteristics, such as unique assemblages of associated fauna and valuable ecosystem services, including fish production, coastal protection, erosion mitigation, pH buffering and nutrient cycling (Coen et al., 2007). These services have been valued at between US$5,500 and $99,000 ha^{-1} (2011 dollars; Grabowski et al., 2012). Because of these valuable services, the protection and restoration of shellfish ecosystems are of interest to coastal managers as one potential natural solution to ameliorating the impacts of climate change, coastal eutrophication and habitat degradation (zu Ermgassen et al., 2016; Cohen-Shacham et al., 2019; McLeod et al., 2019).

Shellfish reefs are globally distributed occupying intertidal and shallow subtidal zones in estuaries and on open coastlines across temperate and tropical environments. Today, however, over 85% of oyster reef ecosystems globally have been lost or degraded (Beck et al., 2011). Mechanisms for losses include: overharvest of shellfish and reef degradation from physical removal or breaking up reefs during harvest, changes in abiotic conditions such as salinity, sedimentation, hypoxia and flow due to upper catchment and shoreline modification, disease and pollution (Holmes, 1927; Kirby, 2004; Beck et al., 2011; Gillies et al., 2018; Pogoda, 2019). Consequently, oyster reef ecosystems are considered one of the most imperilled and threatened marine ecosystems globally (Beck et al., 2011). Although their decline and associated need for conservation is increasingly recognised as a priority amongst conservation groups and professional science networks (e.g. Beck et al., 2011; zu Ermgassen et al., 2016; Fitzsimons et al., 2019; Pogoda et al., 2019; https://www.shellfishrestoration.org.au) there is a ubiquitous absence of protection (be it legal or policy) or global recognition of the threat of ecosystem collapse.

In Australia, oyster reef ecosystems can be formed by at least 14 different oyster and mussel species and occur in both tropical and temperate regions (Gillies et al., 2018). Of these species, there is reliable evidence that reefs formed primarily by *Ostrea angasi* (Australian flat oyster) or *Saccostrea glomerata* (Sydney rock oyster) have undergone considerable decline from historical distributions (Kirby, 2004; Alleway and Connell, 2015; Gillies et al., 2015a, 2018; Ford and Hamer, 2016). Here we provide a description of the ecosystem these species form and complete a risk assessment using the IUCN Red List of Ecosystems framework (https://iucnrle.org/sub-types) to assess the status of shellfish reef ecosystems formed by *O. angasi* and *S. glomerata* oysters. We term the ecosystem the ‘Oyster Reef Ecosystem of Southern and Eastern Australia’ (SEA Oyster Reefs) which comprises of two community sub-type developed by the above species. We assess the entire ecosystem and, where possible, provide specific information for each community sub-type. The risk assessment considers five criteria, each with three sub-criteria, to define numerical thresholds of threat from Least Concern (LC) through to Critically Endangered (CR) (Rodríguez et al., 2015). The approach is consistent with assessments made according to the IUCN Red List of Species and is similar to the assessment process for ecosytems under the Australian Commonwealth Government’s environmental protection legislation (*Environment Protection and Biodiversity Conservation Act 1999*). Assessing the risk of collapse of ecosystems provides vital understanding about the root causes of decline and potential methods for recovery and can inform appropriate governmental and intergovernmental protection levels and mechanisms (Rodriguez et al., 2015).

1.1. Ecosystem description and key biological characteristics

No single global definition of an ‘oyster reef ecosystem’ exists, largely because reef systems differ considerably according to their foundational species, location, surrounding abiotic attributes and biological processes. Kasoar et al. (2015, p. 982) provide the most quantitative and adaptable definition relevant to Australian oyster reef ecosystems: “Bivalve reef [ecosystems] consists of large areas of biogenic habitat, dominated by living bivalves where the complex structure of hard shells supports a distinct community that is persistent through time”. Kasoar et al. (2015, p. 982) then expand on this general definition: “‘large areas’ typically consist of multiple patches, at least some of which are larger than 5 m^2; ‘dominated’ means at least 25% cover of live shell matter across that space − non-living shell (cultch) may further add to habitat structure and to continuity over time, but without new growth they are unlikely to persist; a ‘distinct community’ is one that supports species and interactions that are rare or absent in surrounding communities; and ‘persistent through time’ describes communities that are likely to remain over ‘decadal time scales or longer’”.

Both *S. glomerata* and *O. angasi* provide the physical and biogenic structure and exhibit similar physical forms and biological composition. Structure occurs as either low-profile beds or high-profile reefs, which are developed through clustering of oysters, on soft sediments or hard structures, in high density. These species also support a similar community assemblage consisting of the same or similar functional species of mobile fauna, epifauna, fishes and microbiota (Crawford et al., 2020; McLeod et al., 2020). Because both species provide a similar physical and biogenic structure and similar or identical ecosystem services in coastal environments (Fig. 1) and are the most common reef-forming species in southern and eastern Australia, we considered these as two distinct community sub-types of a single ecosystem.

Based on historical and current observations collected on both community sub-types (Ford and Hamer, 2016; Gillies et al., 2017; McAfee et al., 2016; Keane and Gardner, 2018; Crawford et al., 2020; McLeod et al., 2020) we provide a qualitative description of the physical form and functional features of SEA Oyster Reefs at the patch-scale (i.e. network of reefs within an estuary, its most typical form of occurrence) to aid the delineation of reefs ecosystems compared to other ecosystems (i.e. oyster reefs versus dense populations of oysters within other ecosystems) (Table 1).

Fig. 1. Australian flat oyster (*Ostrea angasi*) sub-community in Georges Bay, Tasmania (left; Photo: C. Gillies, The Nature Conservancy) and Sydney rock oyster (*Saccostrea glomerata*) ecosystem in Hunter River, New South Wales (Right; Photo: S. McOrrie, New South Wales Department of Primary Industries).

1.2. *Abiotic environment and distribution*

The abiotic envelope in which SEA Oyster Reefs ranges from estuarine to full marine waters in moderate to low energy environments (Edgar, 1998; Gillies et al., 2015a). The ecosystem occupies the intertidal and subtidal zone between the mean high tide line to 30 m below sea level, in estuaries, bays, inlets, gulfs and coastal waters from southwestern Western Australia, eastward along the southern coast, including Tasmania, to south-east Queensland south of Bundaberg (Gillies et al., 2018). Oyster reef ecosystems formed by *O. angasi* typically occur subtidally, from low intertidal to a depth of 30 m and favour fully marine salinities. *S. glomerata* typically occur in the intertidal zone within estuaries although historic evidence suggests reefs were common in subtidal areas down to at least 10 m (Smith, 1981; Diggles, 2013) and prefer more estuarine salinities (10–35 ppt) (Dove and O'Connor, 2007). Community assembles are functionally similar amongst both community sub-types with some overlap in species composition where ranges overlap (Crawford et al., 2020; McLeod et al., 2020).

1.3. *Current typological classifications*

Shellfish Beds and Reefs are classified under the global IUCN Global Ecosystem Typology (Keith et al., 2020) as ecosystems occurring within the Marine Realm, Marine Shelves Biome (M1.4). In Australia, oyster reef ecosystems can be classified under the National Intertidal/Subtidal Benthic (NISB) habitat classification scheme (Mount et al., 2007) and Interim Australian National Aquatic Ecosystem Classification Framework (Aquatic Ecosystems Task Group, 2012) as occurring in marine and estuary systems on unconsolidated substrate with a Structural Macrobiota (SMB) dominated by a filter feeding assemblage. The ecosystem is classified under the Ramsar Classification System for Wetland Type (Ramsar, 2012) and is defined as E7 'Bivalve (shellfish) reefs'.

1.4. *Key natural processes*

Oyster reefs typically form as successive generations of bivalves settle and grow on top of one another and persist by several key processes and interactions (Fig. 2). The availability of clean substrate is a key requirement for regular recruitment and reef persistence, with oysters showing a preference for attaching to other living oysters (Rodriguez-Perez et al., 2019). This process aids the physical development of reefs and creation of a positive shell budget where new oysters settle onto live or dead oysters, elevating the reef from the surrounding substrate. A high spawning biomass, where survival of settled larvae through to maturity is greater than adult mortality is required to support reef growth and maintain dense aggregations (Powers et al., 2009).

The location of reefs and beds within an area can shift through time (across decadal time scales) and geological and Aboriginal cultural evidence of food middens indicates the potential of populations to persist for very long (at least centennial) time periods in a single location (Edgar and Samson, 2004; Gillies et al., 2015a). A combination of environmental parameters govern the position of oyster reef ecosystems within a seascape, including: wave exposure and currents, sedimentation, salinity, food availability and suitability of substrate for settlement. Both oyster species are subject to diseases, which are known to inflict significant mortality in aquaculture settings (Winter Mortality Syndrome, Queensland Unknown Disease (QX) for *S. glomerata*; *Bonamia exitosa* for *O. angasi*) (Nell, 2001; Carnegie et al., 2014).

A key feature and biological process of oyster reef ecosystems is their capacity to capture food and nutrients from the water column and transfer them to the benthos, a process known as bentho-pelagic coupling (Newell, 2004). The drawdown of plankton and seston from the water column through the filter feeding of oysters and the subsequent production of oyster biomass, faeces and pseudo faeces, cleans the water-column and enriches the benthos with nutrients that underpin the

Table 1
Semi-qualitative reef attributes (physical form and functional features) of the Oyster Reef Ecosystem of Southern and Eastern Australia which may aid the delineation of reefs ecosystems versus alternate ecosystems with oyster populations.

Attribute	Fully functional reef ecosystems	Partially functional reef ecosystems	Oyster populations within alternate ecosystems	Oyster density (μ m^2 ± s.d.) and sources
1. Oyster density				
O. angasi	>50 live oysters/m^2	50-10 live oysters/m^2	<10 live oysters/m^2	Jones and Gardner (2016) 18.3 ± 16.7 Crawford et al. (2020) 20 ± 1 to 229 ± 7
S. glomerata	>500 live oysters/m^2	500-100 live oysters/m^2	<100 live oysters/m^2	Summerhayes et al. (2009) 940 ± 251 McLeod et al. (2020) 10.2 ± 3.3 to 740.5 ± 15.8
2. Oyster coverage/ dominance	Oysters and oyster shell are the primary physical feature in seascape	Oysters and oyster shell partially cover seascape, interspersed with other physical, biological features	Oysters and oyster shells minor feature in seascape	Powers et al. (2009) Schultz and Burke (2014)
3. Shell budget and reef height	Increasing or stable spatial extent and/or height. Patches consist of a mix of live oysters and dead shell.		Little or no evidence of stable shell structure	Powell et al. (2006)
4. Patch number and size	Multiple patches of reef with vertical relief from surrounding substrate, reef patch sizes ≥ 5m^2		Few or no discrete oyster reef/shell patches	Jones and Gardner (2016) McLeod et al. (2020)

productivity of benthic fauna and vegetative communities (Dame et al., 1984; Newell and Koch, 2004), while facilitating microbial activity that positively influence nitrogen and phosphate re-mineralization (Kellogg et al., 2013).

1.5. Historical and current threatening processes

Threats to SEA Oyster Reefs mirror global patterns (Beck et al., 2011). Historical threats were primarily unregulated fishing resulting in over-harvest during the first 100 years of European colonisation and the use of destructive fishing equipment such as dredges (Smith, 1981; Nell, 2001). Oyster fishers used dredges, but also hand harvest methods, which broke up, removed or buried oysters and shell resulting in loss of oyster biomass, removal of settlement substrate, a decline in ecosystem function, and ultimately a shift towards an unconsolidated substrate. Abiotic factors such as historical and ongoing changes to land and water use in catchments and estuaries can threaten ecosystem formation and persistence by influencing the environmental conditions of an estuary (e.g. salinity, pH, dissolved oxygen, freshwater flow, tidal dynamics, sedimentation, shoreline availability, auto and allochthonous estuary primary production (Chan et al., 2002; Taylor et al., 2004; Thrush et al., 2004)). These drivers have a direct impact on oyster growth and survival by controlling the degree of smothering, water quality, availability of surface for recruitment, food availability, and predation (Lenihan and Peterson, 1998; Nell, 2001; Brumbaugh et al., 2006; Wasson, 2010; Diggles, 2013; O'Connor et al., 2015). The oxidation of sulfidic floodplain sediments and release of acidic waters ($pH < 6$) into estuaries is particularly widespread in eastern Australia (Sammut et al., 1996) and causes significant mortality and stress in *S. glomerata* (Dove and Sammut, 2007), although oysters may be adapting (Amaral et al., 2011). Floods in historical and contemporary times are catastrophic threats, which can cause physical damage, abiotic changes in estuaries and precipitate the spread of diseases (e.g. QX, Winter Mortality) and parasites such as mudworm (Ogburn et al., 2007; Green et al., 2011; Diggles, 2013; Spiers et al., 2014). Current threats, in addition to the legacy of historical harvesting and catchment disturbance, include disease (described above), climate change (primarily through ocean acidification), altered temperature and salinity and resultant potential loss of suitable abiotic growing conditions (Parker et al., 2009; Gillanders et al., 2011), commercial and recreational fishing (Keane and Gardner, 2018), and removal of available surfaces for colonisation through shoreline modification.

1.6. Definition of ecosystem collapse

Whilst the IUCN Red List of Ecosystems provides a mechanism to assess ecosystem collapse across the extent of the entire ecosystem, we were unable to find a definition of degradation towards collapse at the local level (i.e. at a location – the scale at which most management is undertaken) in the literature for any shellfish reef ecosystem. We therefore provide a definition of ecosystem collapse for a reef system at the location scale derived from our cause-effect model (Fig. 2), from the Interim Australian National Aquatic Ecosystem Classification Framework (Aquatic Ecosystems Task Group, 2012) and common criteria used to measure the success of oyster reef restoration in the United States and Australia (Oyster Metrics Workgroup, 2011; Baggett et al., 2014; Gillies et al., 2017; McLeod et al., 2020).

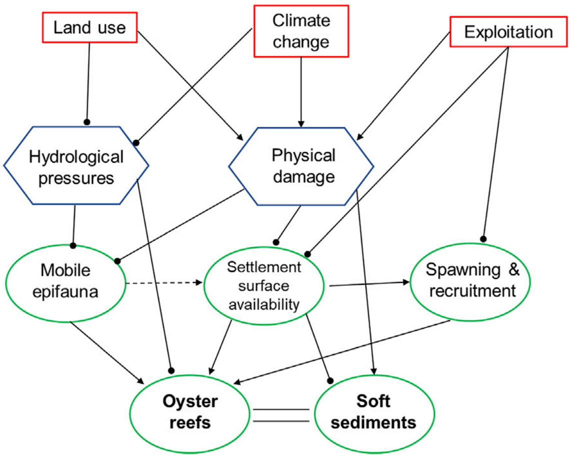

Fig. 2. Cause and effect model for the Oyster Reef Ecosystem of Southern and Eastern Australia. Drivers (red rectangles) such as land use (including shoreline modification), climate change and exploitation influence hydrological pressures (water flow, salinity, pH, thermal, wave exposure) and physical damage (smothering, substrate loss, siltation, abrasion) (blue hexagons), leading to ecological changes in oyster reef structure and community (green ovals). The system alters between oyster reefs and soft sediment communities (double lines) depending on the state of the ecosystem. Line arrows promote positive effect, line circles reduced effect, dashed line may increase effect (i.e. presence of mobile epifauna (e.g. predators) can enhance/reduce surface availability). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

The ecosystem has collapsed when there are no remaining locations dominated by living oysters and oyster shells. Spatial complexity and the presence of hard substrate will have significantly decreased (where not occurring on otherwise hard surfaces (e.g. rock or mangrove roots). Microclimates and local hydrodynamics may also change. Species assemblages will shift from a diverse range of sessile and mobile reef-associated organisms, to a system that is predominantly characterised by infauna and deposit feeders (when shifting to soft sediments) or lower diversity and biomass of reef-associated species when shifting to bare rock/mangrove). Indicators of ecosystem decline at the patch-scale can be observed by measuring density of oysters, oyster recruitment, survival and growth (Table 1).

2. Risk assessment methods

Following the methods of Keith et al. (2013) and guidelines of Rodriguez et al. (2015), we conducted a risk assessment to determine the risk of collapse for SEA Oyster Reefs comprising the community sub-types *S. glomerata* and *O. angasi*. Five criteria and three sub-criteria, developed for the IUCN's Red List of Ecosystems (Rodriguez et al., 2015; https://iucnrle.org/), formed the framework of the risk assessment. These were: *Criterion A*) rates of decline in ecosystem distribution; *Criterion B*) restricted distributions with continuing declines or threats; *Criterion C*) rates of environmental (abiotic) degradation; *Criterion D*) rates of disruption to biotic processes; and *Criterion E*) quantitative estimates of the risk of ecosystem collapse. The sub-criteria in each primary criteria define timeframes for the assessment period (e.g. past 50 years, next 50 years and since 1750), over which decline (or degradation) in ecosystem extent (or function) can be assessed (see Table 2 for all criteria and sub-criteria). Metrics, defined in Keith et al. (2013), were used to assign one of six risk categories to the ecosystem for each sub-criterion and included: data deficient (DD), least concern (LC), near threatened (NT), vulnerable (VU), endangered (EN) and critically endangered (CR).

Table 2
Assessment of threat ranking of the Oyster Reef Ecosystem of Southern and Eastern Australia using the IUCN Red List of Ecosystems criterion.

Criterion	A: Reduction in extent	B: Restricted geographic distribution	C: Environmental degradation	D: Disruption of biotic processes	E: Quantitative analysis	Overall threat ranking (based on highest risk ranking)
Sub-criterion	*1 = Past* 50 *yrs* *2 = Next* 50 *yrs* *3 = Since 1750*	*1 = Extent of Occurrence* *2 = Area of Occupancy* *3 = # threat locations*	*1 = Past* 50 *yrs* *2 = Next* 50 *yrs* *3 = Since 1750*	*1 = Past* 50 *yrs* *2 = Next* 50 *yrs* *3 = Since 1750*	1 = ≤50% in 50 yrs 2 = ≤20% in 50 yrs 3 = ≤10% within 100 yrs	
1	DD	LC	DD	DD	DD	CR
2	DD	EN	DD	DD	DD	
3	CR	VU	VU	CR	DD	

DD = Data Deficient, LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered.

2.1. Sources of data and assessment methods

2.1.1. Criterion A: Reduction in geographic distribution

For Criterion A, we used the published literature sources of Gillies et al. (2015a, 2018), which provide data at the national scale and several other studies which described historical distributions at regional scales (i.e. state jurisdiction: Kirby, 2004; Ogburn et al., 2007; Diggles, 2013; Alleway and Connell, 2015; Ford and Hamer, 2016; Thurstan et al., 2020) as a proxy for ecosystem distribution, since no current or previous distribution maps exist. We assessed historical distributions at the location level with knowledge of present distributions published in Gillies et al. (2015a), Jones and Gardner (2016) and McLeod et al. (2020).

Information from the above studies consisted of a mix of primary and secondary sources that include: early explorer accounts, fisheries and government reports, commercial fishery surveys, first person accounts (published in newspaper articles), archaeological excavations (aboriginal middens), sediment cores, place names and reviews of fisheries legislation. Most of the scientific studies described the ecosystem in the context of wild oyster fisheries/oyster harvest and used a combination of fisheries harvest records, cultural histories, eyewitness accounts and parliamentary records as attesting to and recording the decline of oyster populations and describing the collapse of fishing, but also of oyster reefs. Since very few of these accounts and papers provide information of ecosystem distribution within a location, we measured ecosystem decline as presence/absence of the ecosystem at each recorded historical location.

2.1.2. Criterion B: Restricted geographic distribution

For Criterion B we used ecosystem mapping and distribution data provided by Gillies et al. (2018), which compiles data from several studies (Diggles, 2013; Alleway and Connell, 2015; Gillies et al., 2015a; Warnock and Cook, 2015; Ford and Hamer, 2016; Jones and Gardner, 2016). These studies use methods such as side scan and multibeam sonar, GPS mapping, aerial photos, harvest reports and eyewitness accounts to determine current ecosystem distribution.

Area of Occupancy (AOO) was calculated from these data using a single point for each of the known locations in which the ecosystem is found. A 10 km grid map was constructed over the entire distribution of the ecosystem. We chose to include all grid cells even when the ecosystem occupied <1% because of the small patch sizes associated with the ecosystem (i.e. typically 100 m^2–2000 m^2). The level of uncertainty around this calculation is relatively high. The AOO map and calculations were performed using the GDA94/Geoscience Australia Lambert Projection. To calculate Extent of Occurrence (EOO), a minimum convex polygon (no internal angles are >180°) enclosing all the data was then created in ArcGIS.

2.1.3. Criterion C: Environmental degradation

For Criterion C, we used three variables to quantify environmental degradation of the ecosystem. Firstly, we use catchment land use as an indicator of the variable *sediment load* in estuaries (Chan et al., 2002; Taylor et al., 2004; Thrush et al., 2004). Increased sediment is known to be a primary inhibitor of oyster reef development and persistence, whereby high sediment loads can cause death by smothering, inhibiting oyster settlement or enhancing oyster parasites and disease such as mudworm (Ogburn et al., 2007; Fitzsimons et al., 2019). The eastern and southern coasts of Australia have undergone significant changes in land use since European settlement (Mansergh et al., 2006) and the causal impact this has had on altering river and estuary ecosystems is well known (Prosser et al., 2001).

To determine the level of severity in the indicator *sediment load*, we analysed the most current (2017) Catchment Scale Land Use of Australia data set (https://data.gov.au/dataset/catchment-scale-land-use-of-australia-update-2017). We used percentage of land use change within each associated catchment and applied the relevant IUCN thresholds: i.e. where more than 80% of the catchment had been classified as either 'land for production use' or 'intensive use' this corresponded to a high severity level for that location (i.e. high degree of environmental degradation) and a corresponding severity risk rating of Critically Endangered. Where more than 50% was classified as land under production or intensive use, we classified the location as having a severity risk rating of Endangered and where there was more than 30% of land for production use or intensive use this corresponded to a severity risk rating of Vulnerable. To determine threat extent, we use the proportion of catchments across the ecosystem's distribution which contained a threat rating.

Secondly, we use extent of estuary shoreline modification as an indicator of *substrate simplification*. Modified shorelines can alter or remove abiotic conditions suitable for ecosystem growth and persistence (i.e. elevation, slope, wave energy dynamics, substrate type, availability of hard surfaces). We quantified the percent of shoreline loss by selecting a 2 km buffer around estuaries with historical reefs as the analysis area, then calculated the percentage of different land use types for each estuary. We calculated the percentage of land classified as nature conservation areas/minimal use and the percentage of land calculated as urban intensive uses (including residential, commercial buildings, transport infrastructure) for each estuary within this area. We assigned threat categories to each location using the same method described above.

Thirdly, to assess future threats, we identified the main drivers likely to affect biotic and abiotic interactions of oyster reefs from a broader list of key threatening processes for coastal and estuary systems identified from the Department of Climate Change (2009), Gillanders et al. (2011), Hobday and Lough (2011) and Clark and Johnston (2017) and derived the associated impact of the stressors on oyster reef ecosystems from the literature (see *Historical and Current Threatening Processes* section above, also summarised in Fig. 2 and Table 3).

Table 3
Current and future environmental threats and their impacts on the Oyster Reef Ecosystem of Southern and Eastern Australia. See *Historical and Current Threatening Processes* section for references.

Threat	Future trend	Abiotic response	Biotic response
Climate and weather	Increasing	Altered pH, altered salinity, smothering from sediment associated with floods, reduced water quality, heat stress, loss of hard surfaces for recruitment	Oyster stress, decline in physical oyster condition and mortality, shift towards sediment responsive faunal community, increased (oyster) disease prevalence
Erosion and inundation regime	Increasing	Smothering from sediment, loss of hard surfaces for recruitment, physical disturbance	Oyster stress and mortality, shift towards sediment responsive fauna
Sediment transport	Increasing	smothering from sediment, loss of hard surfaces for recruitment	Oyster stress and mortality, shift towards sediment responsive fauna, increased oyster predator prevalence (e.g. mud worm)
Coastal river and estuary pollution	Increasing	Toxicity, increased bioavailability of pollutants	Oyster and ecological community stress, decline in physical condition and mortality
Flow regimes	Increasing	Altered salinity, water quality, heat stress	Oyster stress and mortality, ecological community stress and mortality
Water abstraction	Increasing	Altered salinity, water quality, thermal stress, stratification	Oyster stress and mortality, ecological community stress and mortality
Low-oxygen dead zones	Stable	Oxygen supply	Mortality, loss of community diversity

Collectively, these three indicators were used to demonstrate plausible relationships between catchment change as the primary driver of several abiotic stressors that are known to affect ecosystem growth and persistence. These connections are highlighted in our ecosystem conceptual model (Fig. 2).

2.1.4. Criterion D: Disruption of biotic processes or interactions

For Criterion D, we selected the biotic indicator *abundance of key species* (oysters) as the primary mechanisms to assess decline in altered biotic interactions. Oyster reefs in their reference condition are characterised by high densities of oysters which provide habitat, shade, food and shelter for a diverse flora and fauna assemblage. Oysters are an ecosystem engineer and loss of oyster biomass to levels defined as a collapsed state (Table 1) disrupts fundamental biotic processes that sustain reef persistence and creation on which most reef-associated flora and fauna rely. Assessment was made by considering (qualitatively) the strength of the drivers identified in Criterion C against published data on the effect of biotic processes and interactions. Where the ratio of oyster recruitment through to reproductive or mature age is higher than oyster mortality, the ecosystem can feasibly exist in a steady state or expand in size and maintain a shell budget. Where recruitment is limited, or when oysters are unable to survive to maturity the ecosystem will either maintain a steady state, or where mortality exceeds recruitment, the ecosystem will decline.

2.1.5. Criterion E: Quantitative analysis that estimates the probability of ecosystem collapse

We did not conduct an assessment against Criterion E, due to the small and isolated number of remaining reefs each occurring in different estuary systems. The complex hydrodynamics associated with estuaries and coarse nature of the available time series data inhibits an ecosystem-wide quantitative assessment of future collapse over the time series of 50–100 years. We therefore classified Criterion E as Data Deficient.

3. Results

The assessment revealed different levels of threat detectable by different indicators from Data Deficient to Critically Endangered, with all of the four main criteria assessed having at least one of the three sub-criteria with a risk rating equalling Vulnerable (Table 2). Overall, the degree of confidence in the data varied (e.g. high degree for Criteria A, 'since 1750') to less confidence (e.g. Criteria D, 'past 50 years'). Two of the four criteria assessed against the 'Since 1750' time category were assessed as Critically Endangered and these were consistent when analysed for both sub-community types. Both sub-community types had similar risk ratings, and met similar criteria for assessment as Critically Endangered, although the *O. angasi* sub-community was assessed as particularly high for several criteria (A,B) because of its highly restricted geographic distribution. Overall, and as per the IUCN Red List for Ecosystems methodology, taking the highest risk rating, SEA Oyster Reefs were assessed as Critically Endangered.

3.1. Criterion A: Reduction in geographic distribution

3.1.1. A1: Reduction in the past 50 years

Gillies et al. (2018) identified seven locations which currently contain SEA Oyster Reefs, only one of which contains the *O. angasi* community sub-type. Two additional locations for *O. angasi* community sub-type have recently been identified in

Tasmania and Victoria (pers. obs) but these have yet to be assessed. Likewise, in New South Wales, anecdotal evidence exists for *S. glomerata* reefs in other locations (NSW DPI, 2019) not identified by Gillies et al. (2018), yet these have yet to be mapped or verified as reef ecosystems. Current verified best estimates therefore indicate that only seven (but potentially nine) of an estimated 178–303 (lower-upper estimates, Gillies et al., 2018) historical locations (i.e. bays, estuaries, embayments) contain a remnant of the ecosystem (inclusive of both community sub-types).

Ford and Hamer (2016) provide evidence that limited oyster harvesting (30 tonnes per year) still occurred in Port Phillip, Victoria, up until the mid-twentieth century indicating that reefs or dense beds were still present around 50 years ago in that region, although the extent to which these were *O. angasi* compared to *Mytilus* (*edulis*) *galloprovincialis* (blue mussel) which were also harvested at the time is unknown. In all other locations, reports of collapse for the ecosystem had occurred prior to 1950 (Kirby, 2004; Diggles, 2013; Alleway and Connell, 2015; Ford and Hamer, 2016; Gillies et al., 2018; Thurstan et al., 2020). Despite the potential for decline within the last 50 years, evidence of recent loss is limited and further work needs to be undertaken to address this knowledge gap. We therefore conclude that the status of the ecosystem under this sub-criterion (i.e. past 50 years) is Data Deficient.

3.1.2. A2: Reduction over the next 50 years

We infer the risk of future ecosystem collapse over the next 50 years will be based largely on the extent to which further environmental degradation occurs, since the primary historical stressors (harvesting through dredge methods, massive land use change) have largely abated and are unlikely to reoccur in all Australian states where the ecosystem is found. There was also insufficient data to project a quantitative estimate of the future distribution and we assess the status here as Data Deficient.

3.1.3. A3: since 1750

Gillies et al. (2018) described the decline in the *O. angasi* sub-community from 118 historical locations (most conservative estimate) to just one location known today, a decline of over 99%. For *S. glomerata* community sub-type, only 6 of 60 historical locations (conservative estimate) have been identified, resulting in a 90% decline. Collectively for the ecosystem, the most optimistic national assessment indicates seven of 178 historically known locations still occur today, resulting in a decline of 94%. Gillies et al. (2018) conclude that ecosystem decline occurred primarily over a 150-year period from 1800 to 1950 which coincided with the peak wild oyster harvest fishery, landscape modification for the primary purpose of agriculture, forestry and urbanization, and industrialization of coastal areas and estuaries across south-eastern Australia (Gillies et al., 2015a, 2018).

Kirby (2004) described the collapse of all natural oyster fisheries (primarily *S. glomerata*) in New South Wales and southeast Queensland by 1910 which is similar to Ogburn et al.'s (2007) estimate that New South Wales subtidal oyster reefs (primarily *S. glomerata*) were in decline by 1880. In Victoria, Ford and Hamer (2016) describe >90% loss of *O. angasi* reefs in Port Phillip, Western Port and Corner Inlet coastal systems by 1860, although oyster fisheries were able to continue at much lower biomass until 1970. Alleway and Connell (2015) describe a collapse of the *O. angasi* fishery and reefs across at least 1500 km of coastline in South Australia by 1944. Warnock and Cook (2015), describe the loss of oyster beds (*O. angasi*) in southwest Western Australia estuaries by 1940. At the estuary scale, Diggles (2013) describes collapse of subtidal *S. glomerata* communities by 1920 and Edgar and Samson (2004) indicate a 100% decline of *O. angasi* beds in the D'entrecasteaux Channel, Tasmania, by 1930.

Based on the weight of evidence from the above studies, the rate of ecosystem decline after European settlement was rapid and directly associated with an increase in commercial harvest which had largely ceased across the ecosystem's distribution by 1920. We therefore assess the status of the ecosystem under sub-criterion A3 as Critically Endangered (including for both community sub-types) with a high degree of confidence.

3.2. Criterion B: Restricted geographic distribution

3.2.1. B1: Extent of Occurrence

The minimum convex polygon encompassing all confirmed remaining sites (7) encompasses an Extent of Occurrence (EOO) of 73,250 km^2 (Fig. 3), which, when using the process of Bland et al. (2017), is considered as 'Least Concern'. We also re-ran the assessment separately for the *S. glomerata* sub-community which provided an EEO of 47,541 km^2. The current single location known for *O. angasi* would equal an EOO of <1 km^2 (Keane and Gardner, 2018).

Sub-criteria B1–B3 also requires an assessment of the number of threat-defined locations (defined as a geographically or ecologically distinct area in which a single threatening event can rapidly affect all occurrences of an ecosystem type; Bland et al., 2017). For the *O. angasi* sub-community, only a single population is known to occur in north-eastern Tasmania making this sub-community type extremely vulnerable to single catastrophic events such as floods, droughts, storms, and potentially, recruitment failure if the existing commercial oyster fishery were to cause local depletions (Keane and Gardner, 2018). We therefore categorized this region as a single threat-defined location. For the *S. glomerata* sub-community, populations in New South Wales and south-eastern Queensland can be exposed to single catastrophic events across the entire region (specifically land and marine heatwaves and droughts) but also other events which can affect one or more catchments (e.g. east coast flooding, hypoxic black water events) at one time but are unlikely to affect the entire ecosystem extent. From a management

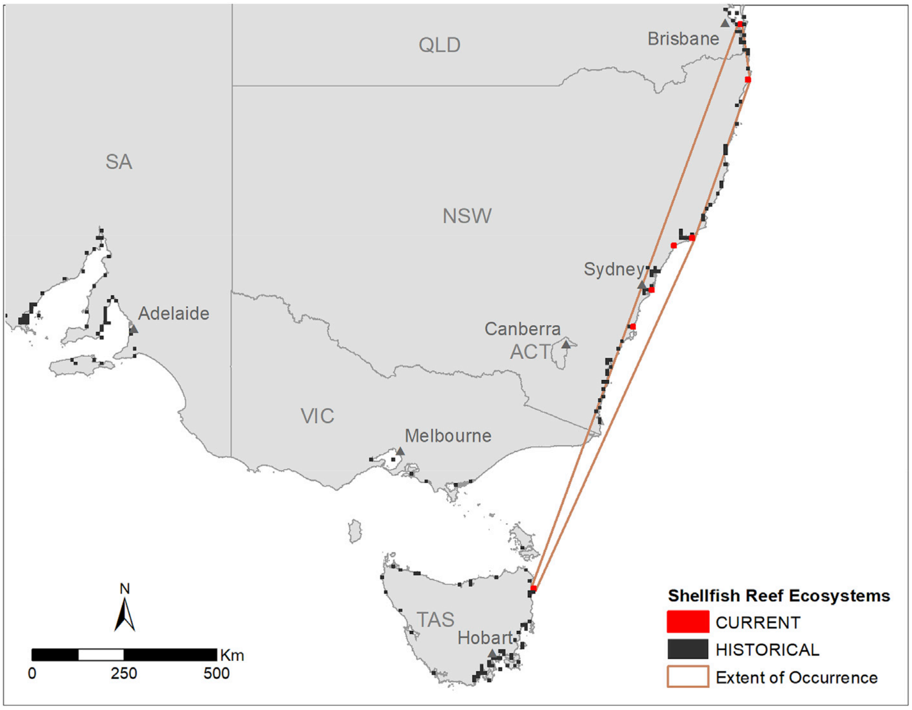

Fig. 3. Extent of Occurence for the Oyster Reef Ecosystem of Southern and Eastern Australia consisting of both community sub-types. Data derived from Gillies et al. (2018).

view, in New South Wales, all reef locations are located within the Coastal Vulnerability Area, a spatial zone defined under the New South Wales *Coastal Management Act 2016*, which is identified largely because it has the same coastal threats and vulnerability. Regardless of whether one threat-defined location (entire region-heatwaves and droughts) or six threat locations (catchments-floods and blackwater events) are identified, the risk rating would be the same (i.e. $\leq$ 10, Vulnerable). When considering the EOO for the SEA Oyster Reefs (comprising both community sub-types) the ecosystem was classified as Least Concern (Extent of Occurrence is > 50,000 km^2). When considering the community sub-types individually the *S. glomerata* community sub-type was classified as Vulnerable and, based on the extremely low EOO and single threat-location, we classified the *O. angasi* community sub-type as Critically Endangered.

3.2.2. B2: Area Of Occupancy (AOO)

We identified seven out of a total of 193 cells (3.6%) as occupied by the ecosystem (Fig. 4), although in several estuaries the area of occupancy is likely to only occupy <1% of the grid cell (i.e. less than 1 km^2 as indicated by McLeod et al. (2020), demonstrating the ecosystem is currently severely fragmented. Yet because of the uncertainty of the total area occupied at each location (i.e. not all reef patches were mapped at each location by McLeod et al. (2020) we were cautious and included all cells within our assessment. A grid count of seven cells indicates a risk rating of Endangered ($\leq$20 cells and less than five threat locations, included – see B1 above). We therefore assess the risk rating for B2 as Endangered, with *S. glomerata* community sub-type (6 grid cells) assessed as Endangered and *O. angasi* (1 cell) Critically Endangered.

3.2.3. B3: Number of threat-defined locations

The ecosystem can be considered Vulnerable (the only threat category available in this sub criterion) because it meets the criteria of occurring in less than five threat-defined locations and both community sub-types are vulnerable to complete collapse from single catastrophic events (described above) which could occur in the immediate future and over a short period of time.

3.3. Criterion C: Environmental degradation

3.3.1. C1: The past 50 years

Due to the difficulty in linking drivers and threats relating to biotic degradation across the ecosystem's entire extent to the past 50 year time horizon only, we were unable to complete an analysis for this sub-criterion and we classified this as Data Deficient.

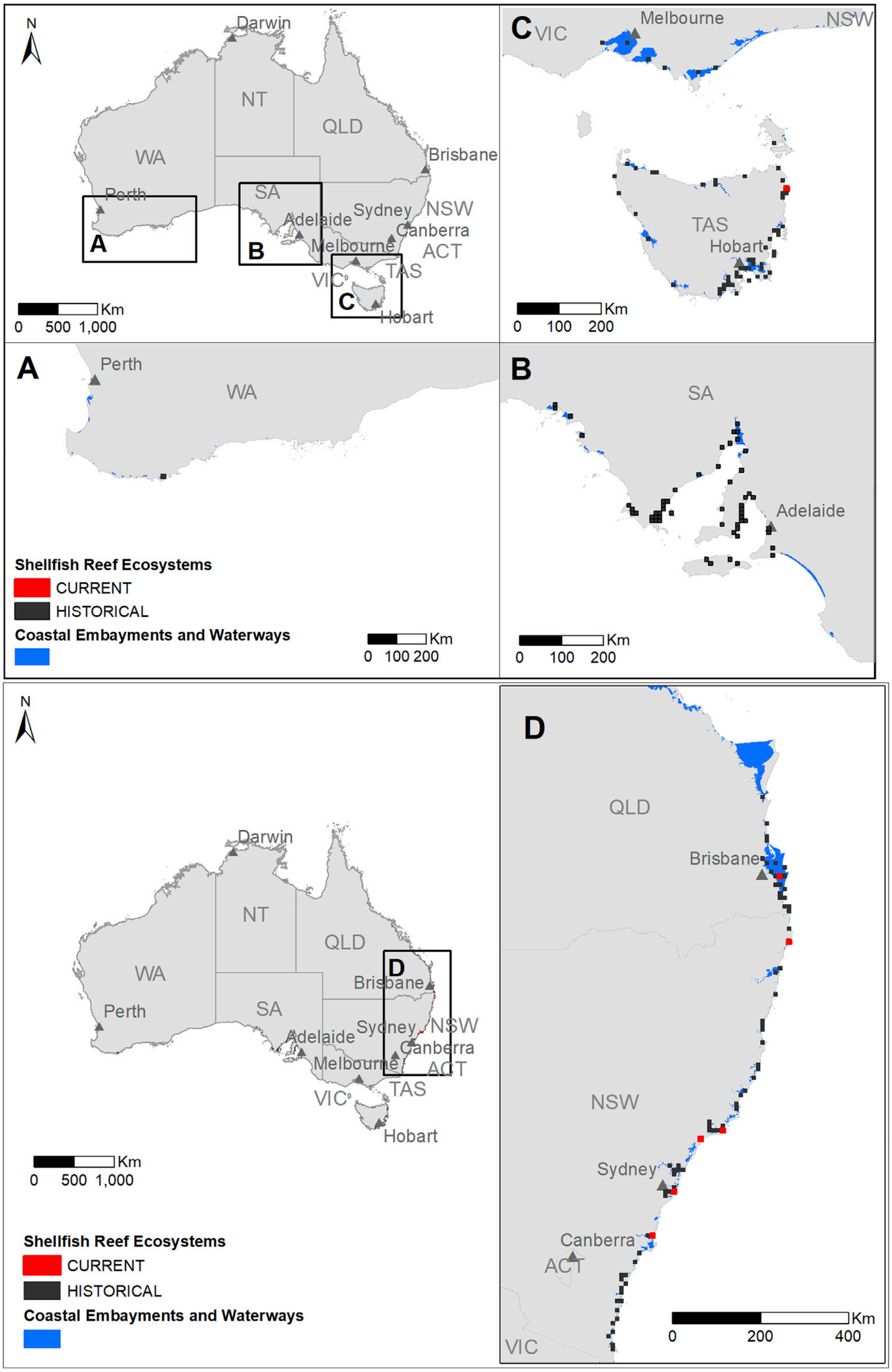

Fig. 4. Current extent and historical distribution and Area of Occupancy of the Oyster Reef Ecosystem of Southern and Eastern Australia, with each cell representing 10 sq km. Coastal embayments in blue represent potential ecosystem occupation. Data derived from Gillies et al. (2018). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.3.2. C2: The next 50 years

Of the 25 coastal and estuary drivers and threats identified in Australia by Clark and Johnston (2017), seven have the potential to cause ecological collapse of SEA Oyster Reefs by altering conditions that control both the abiotic and biotic conditions required for ecosystem persistence (Table 3). All but one of these threats (low-oxygen dead zones) are expected to deteriorate further in the future in southern and eastern Australia (Gillanders et al., 2011; Cark and Johnston, 2017), posing a higher risk of collapse to the ecosystem compared with today. In particular, 'climate and weather' is considered to have a 'very high impact' on Australia's bays and estuaries, with mean annual rainfall expected to decrease, storm events increase and sea level rise expected to be higher for south-eastern Australia compared to the global average (Department of Climate Change, 2009; Hobday and Lough, 2011; McInnes et al., 2016). These current and future threats which are expected to increase in intensity in the near future, provide a high level of confidence that the ecosystem is at risk of future collapse within the next 50 years. However, we assessed this criterion as Data Deficient because whilst there is certainty that threats will increase in the near future and are likely to have an impact on oyster populations, we were unable to determine the likely adaptive response of the ecosystem (see Discussion).

3.3.3. C3: since 1750

The relative severity of catchment modification as a driver of the abiotic stressor *sediment supply* equated to threat rankings ranging from Least Concern to Critically Endangered, with 90% of all extant sites (n = 198) assessed as Vulnerable or higher (Table 4). This resulted in a Vulnerable risk rating for this indicator because the assessment meets the threshold of >30% degradation across >80% of the ecosystem extent. Similarly, 86% of catchments (n = 178) assessed for estuary shoreline modification as a driver of *substrate simplification* had a high degree (>50% degradation, Table 4), resulting in an overall risk rating of Vulnerable. Collectively for these two indicators our assessment suggests a plausible threat of historical environmental degradation as a result of catchment and estuary shoreline modification across most of the extent of the ecosystem. We thus assessed this criterion as Vulnerable with a high degree of certainty.

3.4. Criterion D: Disruption of biotic processes

3.4.1. D1: The past 50 years

Only one study in a single location (Sydney) has observed an increase in natural oyster (*S. glomerata*) abundance over the last 50 years (Birch et al., 2014). In aquaculture, oyster production has declined by half since peak production in mid 1970s, in part attributed to disease (QX, Winter Mortality Syndrome) and declining water quality (White, 2001; NSW DPI, 2016). Whilst these drivers are likely to also have affected wild oyster populations, unfortunately, no similar long-term assessment of wild oyster populations or recruitment have been published. We therefore assess this sub criteria as Data Deficient.

3.4.2. D2: The next 50 years or any 50-year period

Projections of distribution and biomass of oyster ecosystems in the next 50 years are limited and the status of the ecosystem under this sub-criterion was considered Data Deficient.

3.4.3. D3: Since 1750

Several studies have previous documented collapse of the ecosystem as a result of oyster extraction (Ogburn et al., 2007; Lergessner, 2008; Diggles, 2013; Alleway and Connell, 2015; Gillies et al., 2015a, 2018; Ford and Hamer, 2016, Thurstan et al., 2020), though only three have quantified decline in oyster abundance or biomass. Thurstan et al. (2020) document total

Table 4
Levels of catchment degradation and estuary shoreline modification corresponding to IUCN risk criteria for current shellfish reef locations and for all current and previously known locations of the Oyster Reef Ecosystem of Southern and Eastern Australia. Categories: 0–30% = Least Concern; 31–50% = Vulnerable; 51–80% = Endangered; 81–100% = Critically Endangered.

Location	% catchment modification	Catchment rating	% estuary shoreline modification	Shoreline rating
Current shellfish reef locations				
Moreton Bay, Queensland	7	LC	75	EN
Richmond River, New South Wales	67	EN	76	EN
Port Stephens, New South Wales	49	VU	25	LC
Hunter River, New South Wales	64	EN	79	EN
Botany Bay, New South Wales	77	EN	89	CR
Crookhaven River, New South Wales	46	VU	34	VU
Georges Bay, Tasmania	42	VU	34	VU
All current and previously known sites (% of total)	(N = 198)		(N = 178)	
	15.2 (30)	CR	19.1 (34)	CR
	39.4 (78)	EN	51.1 (91)	EN
	35.4 (70)	VU	15.7 (28)	VU
	10.1 (20)	LC	14.0 (25)	LC

collapse of the ecosystem, estimating a 96% decline in *S. glomerata* fisheries production in 2016 compared to the peak of the fishery in 1891. Alleway and Connell (2015) document a similar (96%) decline in harvest records for *O. angasi* between 1886 and 1944 and Ogburn et al. (2007) indicate a 66% decline in both *S. glomerata* and *O. angasi* production in New South Wales.

It was relatively common for historical accounts to describe vast oyster systems ranging from several hundred square meters in length to several kilometers which were intensively harvested for oysters. For instance:

The Fisheries Inspector for Moreton Bay, Fison (1884) reported for *S. glomerata* in Pumicestone Passage, Queensland:

> “33 thousand bags of oysters have been taken, they being in some places four and five feet deep, Mr Freeman having informed me that he has made his boat fast to a stake, and dredged for six weeks”

The New South Wales, Royal Commission on Oyster Culture (1876-7) (New South Wales, 1877) reported for *S. glomerata* in Port Stephens, New South Wales:

> “In the 1860’s a man could work his warp stake into the bed and not leave that spot for sixteen or twenty days, getting fifteen to twenty bags a day all that time. For a long time ten to twelve or even fifteen boats were so employed until only three or four bags could be got… some came back in about three years only to get at most six or seven bags per day”.

The Illustrated *Australian News* (Anon.) (7 November 1891, pp. 8–9) reported for *O. angasi* in Port Albert, Victoria:

> “An account of oyster dredging offshore from Corner Inlet describes an oyster bank ‘from Shallow Inlet towards Wilson Promontory for a distance of 12 miles’ and another ‘3 miles long beginning at the (Corner) Inlet’”

Harvest records, whist not comprehensive, provide an insight into the extent of oyster biomass (typically mature oysters) extracted during previous commercial harvest. For instance, in Western Port, Victoria, during the mid-1850s, 1.2 million dozen oysters were removed per year (Ford and Hamer, 2016). In southeast Queensland, harvest records began in 1874, with an estimated peak in 1891 recording removal of 2–3.65 million dozen oysters per year (Thurstan et al., 2020) and in South Australia, during the 1880s over 100,000 dozen oysters were harvested per year (Alleway and Connell, 2015). Further examples from individual estuaries and industries can be found in Gillies et al. (2015a, 2018, Table 3) and Thurstan et al. (2020). In all circumstances the wild harvest industry collapsed, which often prompted early attempts at aquaculture and ranching (e.g. the laying down of oysters or substrate; Roughly, 1922), before modern cage aquaculture begun in the early 1950s.

A lack of modern data on oyster densities from historical locations and quantitative estimates on historical abundance or biomass precluded a quantitative assessment of decline for known sites. Nonetheless, since the above studies describe extensive reef systems that were intensively harvested across the entire extent of the ecosystem and with most of these studies concluding total collapse of the ecosystem primarily as a result of oyster harvest, we believe there is sufficient evidence to reasonably deduce that the relative severity related to loss of oyster biomass causing ecosystem decline is $\geq$ 90% of past biomass (all studies indicate ecosystem collapse through loss of oysters) and the extent of threat was $\geq$90% of past extent (studies cover the full geographic range of the ecosystem). We therefore assessed the status of the ecosystem under this subcriterion as Critically Endangered with a medium degree of confidence.

4. Discussion

4.1. Status of the Oyster Reef Ecosystem of Southern and Eastern Australia

We assessed the conservation status of the Oyster Reef Ecosystem of Southern and Eastern Australia using the IUCN framework and determined that the ecosystem (including both community sub-types) should be classified as Critically Endangered, the most severe risk rating. Risk ratings ranged across all threat category types, from a Critically Endangered assessment given for Criterion A: Reduction in Extent (since 1750) and Criterion D: Disruption of Biotic Processes (since 1750), through to Least Concern for Criterion D: Disruption of Biotic Processes (past 50 years). Overall the ecosystem met the listing requirements for all criteria (with the exception of Criterion E: Quantitative Analysis, which we were unable to assess), but not for all sub-criteria. The level of confidence also varied among and within criteria. For instance, we found sufficient evidence to quantify the decline in ecosystem extent and oyster biomass throughout the 1800s (largely due to the well documented decline in the wild oyster harvest industry), yet there was little information on the extent of decline over the last 50 years. This result validated Alleway and Connell (2015) observations of shifting baselines for shellfish ecosystems related to loss of memory in recent generations where the general visibility and awareness of oyster reef ecosystems, predominantly over the past 50 years, has been low.

Our assessment and the IUCN Red List process may be of value for other shellfish ecosystems, particularly those that are likely to have undergone significant decline (Beck et al., 2011) and are actively being restored, such as *O. edulis* in Europe, *O. chilensis* and *Perna canaliculus* in New Zealand, *C. virginica* and *O. lurida* in the United States and *C. hongkongensis* in Hong Kong (Fitzsimons et al., 2019). A detailed understanding of ecosystem definition, collapse thresholds and ecological risks can help to inform priority locations for protection and restoration and assist with developing methods for restoration by describing key ecosystem functions and structural attributes, which can guide the development of reference models (Gillies et al., 2017). Even if an ecosystem assessment does not meet any risk thresholds, undertaking the process itself can reveal new insights into the ecosystem (including gaps in understanding), and if undertaken regularly, can be used to monitor the status of the ecosystem over time (Alaniz et al., 2019). We also surmise the high ecoloigcal value yet relatively small and patchy nature of the ecosystem is representative of the concept of 'small natural features' such as desert springs, bat caves, temporary pools and coral heads which represent managment challenges but also novel oportunties for their protection and restoration (Hunter et al., 2017).

A significant gap in our understanding of this ecosystem is how it will respond to future threats, particularly from climate change. Stressors such as altered water flow, salinity, hypoxia, heat stress and ocean acidification are already increasing or expected to increase in Australian estuaries (McInnes et al., 2016; Clark and Johnston, 2017), yet there is an insufficient number of studies that can confidently predict how estuarine, and particularly shellfish, ecosystems are likely to respond (but see Watson et al., 2009; Gillanders et al., 2011; McAfee et al., 2017; Parker et al., 2017). SEA Oyster Reefs have the potential to migrate within an estuary and could conceivably colonise new estuaries to avoid stress and remain within physiological thresholds, but this is assuming sufficient substrate and oyster biomass is available for local recruitment, settlement and reef creation. We suggest future research should prioritise the development of climate response ecosystem models to understand whether changing climatic factors will exacerbate the identified risk of total collapse and to help identify areas for future protection and management.

There is growing anecdotal evidence that a number of unmapped *S. glomerata* reefs may exist in New South Wales (NSW DPI, 2019) which still require verification as oyster reefs. Oyster reefs may also be establishing on abandoned oyster leases and these are the focus of new restoration sites by the NSW Government (Kylie Russell, NSW DPI, pers. comm.). We suggest that verification of *S. glomerata* reefs in NSW should be prioritised and the *S. glomerata* community sub-type subsequently re-assessed. We note though that in order for the assessment to downgrade from its current assessment as Critically Endangered for Criteria A, the number of validates sites would need to more than double (>15), but this would likely not affect the over rating of Critically Endangered due to the significant historical loss.

4.2. Implications for conservation listing

The assessment of SEA Oyster Reefs as Critically Endangered, has implications for listing under environmental legislation in Australian jurisdictions. Listing under threatened species/communities or related legislation confers a number of important benefits to the ecosystem. These benefits can include: 1) preventing or limiting direct physical destruction/degradation of the system, 2) recognising, listing or addressing threatening processes that might be having an indirect role in degradation, and 3) prioritising and financing conservation and restoration activities related to the ecosystem. Furthermore, the assessment process can assist in identifying appropriate conservation policies that address specific ecosystem risks highlighted by each criterion (Alaniz et al., 2019).

Australia is a federated nation, and environmental law rests primarily with the states and territories (sub-national governments), with some overlapping national government responsibilities (such as for nationally threatened ecological communities). As such, and as there were no distinct differences in our threat assessments between states, listing SEA Oyster Reefs under relevant legislation should be a high priority. Not all Australian states have legislation that enables listing of threatened marine ecological communities. The most relevant current legislation for listing is as follows: Australian Government (national level) – *Environment Protection and Biodiversity Conservation Act 1999* (listing application accepted for assessment in 2018); Western Australia – *Biodiversity Conservation Act 2016*; South Australia – *Fisheries Management Act 2007*; Victoria – *Flora and Fauna Guarantee Act 1988*; Tasmania – *Nature Conservation Act 2002*; New South Wales – *Biodiversity Conservation Act 2016*; and Queensland – *Nature Conservation Act 1992* (critical habitat listing).

Despite the risk of ecosystem collapse for SEA Oyster Reefs, shellfish reefs may be one of the most restorable marine ecosystems globally. Australia's coastal environments have experienced extensive environmental change over the past 200 years, yet Australia's east coast oyster populations have demonstrated resilience to environmental stressors (e.g. McAfee et al., 2017) and readily adhere to most hard substrates. Restoration efforts in Australia and the United States demonstrate that through active restoration methods including the addition of settlement substrate and oyster larvae, many 100s of hectares can be restored within single systems (Schulte et al., 2009; Fitzsimons et al., 2019; https://www.shellfishrestoration.org.au/). The environmental, economic and social benefits of undertaking such restoration are well documented (Coen et al., 2007; Grabowski et al., 2012; Kroeger, 2012; McLeod et al., 2019) and interest in scaling-up marine ecosystem restoration is growing (e.g. Fitzsimons et al., 2015; Gillies et al., 2015b). These studies and the prominent risk of total collapse identified in this study provide a compelling case for new investment that can arrest, and potentially reverse, the decline of the ecosystem.

Declaration of competing interest

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

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Appendix A. Supplementary data

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