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Stable isotopes infer the value of Australia's coastal vegetated ecosystems from fisheries

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Abstract

Wild capture fisheries provide substantial input to the global economy through employment and revenue. The coastal zone is especially productive, accounting for just 7% of the total area of the ocean, but supporting an estimated 50% of the world's fisheries. Vegetated coastal ecosystems—seagrass meadows, tidal marshes and mangrove forests—are widely cited as providing nutritional input that underpin coastal fisheries production; however, quantitative evidence of this relationship is scarce. Using Australia as a case study, we synthesized fisheries stable isotope data to estimate nutritional input derived from coastal vegetated ecosystems and combined these “proportional contribution” estimates with total annual catch data from commercial fisheries to determine species-specific dollar values for coastal vegetated ecosystems. Based on the data from 96 commercially important fish species across Australian states (total landings 14×10^6 tonnes pa), we provide a conservative estimate that Australia's coastal vegetated ecosystems contribute at least 78 million AUD per year to the fisheries economy. Two thirds of this contribution came from tidal marshes and seagrasses that were both equally valued at 31.5 million AUD per year (39.4%) followed by mangroves at 14.9 million AUD per year (18.6%). The highest dollar values of coastal ecosystems originated from eastern king prawn (*Melicertus plebejus*) and giant mud crab (*Scylla serrata*). This study demonstrates the substantial economic value supported by Australia's coastal vegetated ecosystems through commercial fisheries harvest. These estimates create further impetus to conserve and restore coastal wetlands and maintain their support of coastal fisheries into the future.

KEYWORDS

ecological values of ecosystem services, ecosystem services, monetary valuation, quantification of natural capital, socio-ecological and economic benefits of natural capital to human well-being, systematic quantitative literature review

1 | INTRODUCTION

Seagrass, mangrove and tidal marsh ecosystems are increasingly recognized for the range of ecosystem services they provide. This includes carbon sequestration (Macreadie et al., 2017), coastal

protection (Duarte, Losada, Hendriks, Mazarrasa, & Marbà, 2013), filtration of nutrient run-off (Valiela & Cole, 2002), sustaining biodiversity (Ward, Tockner, & Schiemer, 1999), and providing habitat and food for various fish species (Bloomfield & Gillanders, 2005). However, these ecosystems are heavily impacted by climate change,

coastal development, eutrophication, invasive species and agricultural nutrient run-off. These anthropogenic stressors contribute to modification or degradation of these coastal ecosystems and a reduction in the ecosystem services they provide (Geselbracht, Freeman, Birch, Brenner, & Gordon, 2015; Lotze et al., 2008; Waycott et al., 2009).

Ecosystem services refer to the variety of benefits that humans derive from ecosystems. Ecological values of ecosystem services are often derived from ecosystem functions (e.g., habitat provision for fisheries, carbon and nutrient cycling) that incorporate integral biological components of ecosystems (Berg, Mineau, & Rogers, 2016; Ghaley, Porter, & Sandhu, 2014; Martín-López, Gómez-Baggethun, García-Llorente, & Montes, 2014). The economic values of ecosystem services, however, are normally expressed in monetary units and assigned to the services themselves, that is to the consumable human benefit. Estimating economic outputs derived from coastal ecosystem services has proven to be useful for raising awareness, communicating knowledge and justifying and assessing conservation measures (Costanza et al., 2014). While the realised benefit depends on human demand and use of the service, its provision relies on ecosystem production, including a range of ecosystem functions (e.g., combined primary and secondary production; Boerema, Rebelo, Bodi, Esler, & Meire, 2017). For example, wild capture fisheries rely

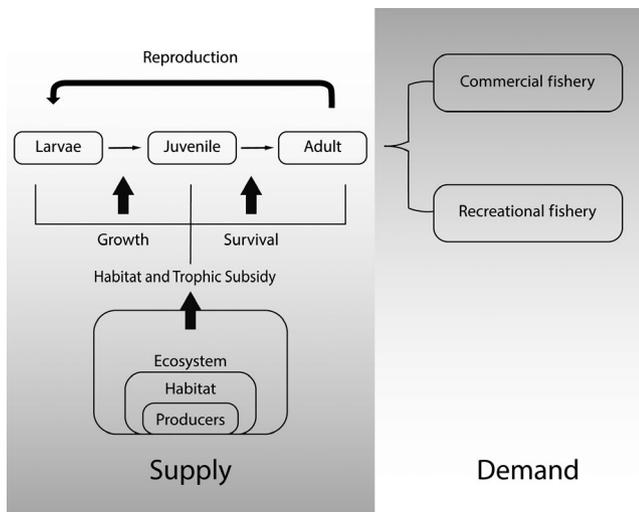


FIGURE 1 Conceptual illustration of fisheries ecosystem services by ecosystem production (supply) and fish catch (demand). In the natural world, primary producers form the basal layer of food webs and are nested within habitats that are nested within ecosystems. Ecosystems provide habitat and trophic subsidy in the form of nutrition to fish production. Habitat availability and trophic subsidy both affect growth and survival probability of fish at all life-history stages (from larvae to juvenile and adult). Habitat availability and trophic subsidy from ecosystems increase growth and improve survival as fish decrease vulnerability to predation with increasing size. Growth and survival in turn affect reproductive output as fish reach maturity faster resulting in more spawners. Adult fish catch is the main consumable human benefit of fisheries ecosystem services and is determined by species-specific market demand

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on ecosystem production (supply) in the form of nutrition and habitat provision, whereas the service itself is realized in the form of catch (demand) (see Figure 1 for conceptual illustration).

Global marine capture fishery production has been estimated to be around 81.5 million tonnes per year and provides a significant input to economies throughout the world (FAO, 2016). While it is understood that coastal ecosystems are important to fisheries, estimating the economic value of these services requires some quantitative estimate of the linkage between ecosystems and the fisheries they support (Abrantes, Barnett, Baker, & Sheaves, 2015). For example, Ronnbaack (1999) conducted a synthesis of valuation studies of mangroves through wild capture fisheries and reported values from USD\$ 750 to 16,750 ha⁻¹ year⁻¹ with the highest reported values in Queensland, Australia. A more recent study that used enhancement estimates related to the availability of nursery habitat estimated the mean value of seagrasses across southern Australia to be AUD\$ 23,000 ha⁻¹ year⁻¹ (Blandon & Zu Ermgassen, 2014). For further context, seagrasses were estimated to contribute EUR 606,239 year⁻¹ to the economy of Gran Canaria, eastern Atlantic (Tuya, Haroun, & Espino, 2014). Currently, monetary values of fisheries ecosystem services have mainly been based on catch or visual census information (both adults and juveniles) from target habitats. However, this overlooks the nutritional contribution of ecosystems that actually underlie the existence of healthy fisheries (Othman, Bennett, & Blamey, 2004; Simmonds, 2007).

One way that fisheries scientists have linked coastal ecosystems to fisheries is through measuring energy transfer. Stable Isotopes have been effectively used over the past decades to investigate trophic

ecology of fish and measure how fish derive nutrients from coastal ecosystems (Abrantes & Sheaves, 2009; Kristensen, Kristensen, & Mangion, 2010; de la Moriniere et al., 2003; Smit, Brearley, Hyndes, Lavery, & Walker, 2006; Svensson, Hyndes, & Lavery, 2007). Stable isotope (SI) analysis involves measuring elemental ratios of carbon, nitrogen and occasionally sulphur isotopes ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$) in fish and their environment, allowing input from given environments to be quantified (Abrantes et al., 2015; Belicka et al., 2012; Connolly, 2003). The overall approach relies on the assumption that species differ from one another in terms of their elemental ratios. Furthermore, species-specific isotope ratios propagate through food webs (through direct or indirect consumption) in a predictable fashion, thus making them one of the best and most commonly used methods to study the transfer of organic material through ecological systems (e.g., Cresson, Ruitton, Ourgaud, & Harmelin-Vivien, 2014; Leclerc, Riera, Noël, Leroux, & Andersen, 2014).

Previous stable isotope research has provided a significant contribution to understanding the dynamics of energy flow and functioning of coastal ecosystems (Connolly & Waltham, 2015; Davis, Pitt, Fry, & Connolly, 2015; Hindell, 2006). However, these studies are mainly dealt with site- or estuary-specific scales due to the significant effort, time and resources required for extensive field sampling. Yet the existence of such data presents a unique opportunity to systematically gather, summarize and quantify ecosystem–consumer relationships. In addition to the remarkable potential of stable isotopes to quantify the linkage between functional properties of coastal ecosystems and fisheries catch, only a few recent examples have explored the use of stable isotopes in conjunction with economic analysis. For example, Taylor, Gaston, and Raoult (2018) presented a novel model based on nutritional contribution of tidal marshes and mangroves to fish production combined with estuary wide landing values of fish.

Here, we integrated decades of fisheries stable isotope research with economic analysis to infer coastal ecosystem values to fisheries in Australia with a main focus on seagrass, mangrove and tidal marsh ecosystems. The overall goal of this study was to collate existing stable isotope literature, evaluate patterns in ecosystem contributions to fish production and provide broadscale estimates of the economic value derived from coastal ecosystems through support of fisheries productivity. Specifically, our aim was to (a) systematically gather and quantify proportional contributions of coastal vegetated ecosystems such as seagrasses, mangroves and tidal marshes to fish and prawn production based on established stable isotope relationships in Australia; (b) use state-wide commercial fisheries reports to identify fish of economic relevance and combine proportional contributions of ecosystems with market values of commercially harvested fish; and (c) estimate species-specific dollar values for seagrass, mangrove and tidal marsh ecosystems in Australia. As a result, we directly linked ecosystem production with ecosystem service, that is fisheries catch and highlight ecological and economic values of coastal ecosystems to fish production. To the best of our understating, this is the first continental attempt to summarize fisheries–ecosystem linkages with stable isotopes in conjunction with simple economic measures.

2 | METHODS

2.1 | Systematic review

We conducted a literature review between September 2017 and June 2018 using ISI Web of Science (WoS) to identify studies that had used stable isotopes to investigate interactions between fish and coastal ecosystems in Australia, following a systematic quantitative literature review using the approach of Pickering and Byrne (2014). The following search terms were used in WoS: “fish*” OR “prawn” OR “crab” OR “squid” AND “isotope” AND “Australia” AND “seagrass” OR “mangrove” OR “saltmarsh” OR “tidal marsh”. This yielded a total of 112 peer-reviewed publications for subsequent evaluation (see Figure S1). After completing the review, personal reference alerts were created to ensure that new emerging publications of relevance would not be missed during manuscript preparation process. Additionally, we screened the grey literature by contacting fisheries experts from universities and governmental organizations as well as searched for publications available on fisheries department websites. As a result, we identified two reports from the Fisheries Research and Development Corporation (FRDC) (<http://frdc.com.au/>) that employed stable isotopes to study linkages between fish and coastal ecosystems.

In a subsequent filtering process of the literature, all studies conducted outside Australia were excluded and remaining publications were read in detail. To be included in the analysis, relevant publications had to express proportional contributions of emergent habitats in coastal ecosystems to fish production by a proportional measure. In total, 16 individual publications and two FRDC reports matched the criteria and were incorporated in the analysis (see Appendix S2 as well as Figure 2 for the spread of the studies).

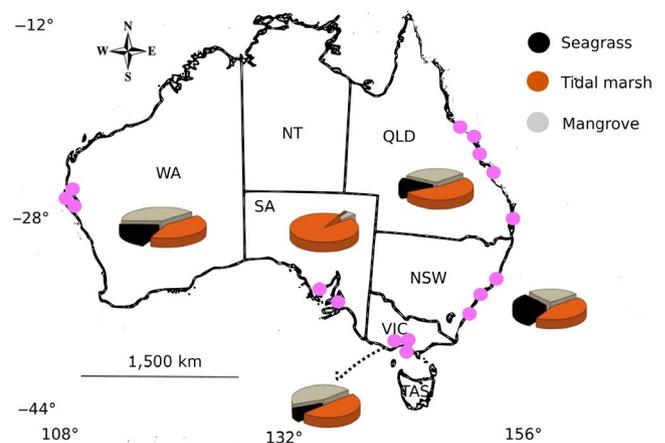


FIGURE 2 Distribution of individual study locations ($n = 15$, full details all studies can be found in Appendix S2), incorporated into our synthesis. NSW, New South Wales; NT, Northern Territory; QLD, Queensland; SA, South Australia; TAS, Tasmania; VIC, Victoria; WA, Western Australia. Pie charts represent the proportion of each ecosystem in states where isotope data were present [Colour figure can be viewed at wileyonlinelibrary.com]

2.2 | Data extraction and proportional contributions

We extracted average species-specific mean and median proportional contributions of primary ecosystems from the literature. Studies reported either the mean (e.g., Hindell & Warry, 2010) or the median contributions (Connolly, Hindell, & Gorman, 2005). As there are no clear ways to estimate median values from means or vice versa, we did not distinguish between median and mean values. In the majority of cases, proportional contributions of ecosystems to fish production were expressed in percentages. If proportions were reported in binomial scale, that is 0–1, then we converted them to percentages (0 = 0% and 1 = 100%) to have a unified measure across all studies.

When proportional contributions were reported for the same fish species in the same Australian state in duplicate studies, then proportional contributions of ecosystems were averaged according to the formula:

$$C_{l,p,s} = \frac{\sum_1^{N_l} C_{n,l,p,s}}{N_l}$$

where $C_{l,p,s}$ is the average contribution (C) of ecosystem p to consumer species s at location l , N_l is the number of studies for location l , and $C_{n,l,p,s}$ is the contribution of ecosystem p to consumer species s reported for study n at location l .

When adding together averaged fish-specific % contributions of ecosystems, then the total often exceeded 100% because ecosystems that were sampled varied between studies (see Appendix S2). To overcome this issue, we normalized the calculation and corrected species-specific ecosystem contributions to match 100%. The calculation outlined below explains how species-specific % contributions of ecosystems were normalized to match 100% without affecting individual weights of ecosystem contributions:

$$C_{n,p,s,l} = \left(\frac{C_{l,p,s}}{\sum C_{l,p,s}} \right) \times 100$$

where $C_{n,p,s,l}$ is the normalized contribution (C) of ecosystem p to consumer s at location l , and $C_{l,p,s}$ is the average contribution (C) of ecosystem p to consumer s at location l .

2.3 | Limitations of mixing models

The stable isotope mixing models used in the original research papers (from which we extracted our data) to calculate proportional contributions come with some inherent limitations that need to be acknowledged (Phillips et al., 2014). For example, many study systems might have source isotope signatures that overlap broadly in isotope space preventing source discrimination. $\delta^{13}\text{C}$ is commonly used as an isotope tracer, but it can struggle to separate certain species of saltmarsh and seagrass as well as some species of saltmarsh and mangroves (Raoult, Gaston, & Taylor, 2018). This adds a degree of uncertainty from the original studies, specifically, in

areas where ecosystems that are tricky to separate are co-occurring. Another important limitation is that the contributions from mixing models are distributions that may have small or large error margins, and in some cases bimodality. Variation in model values is a crucial aspect for interpreting mixing models. Assessments where 90% of model predictions are within 2%–3% of the median suggest consistent reliance on the ecosystem whereas models with large error margins (e.g., 30%) around the median indicate variation and possibly broader diet preference among a population. Both of these shortcomings could be partially alleviated when incorporating sulphur $\delta^{34}\text{S}$ as a third tracer in addition to commonly used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Connolly, Guest, Melville, & Oakes, 2004). As the purpose of this study was to collate published information on contributions from vegetation to fish and invertebrates using stable isotopes, we acknowledge the potential limitations of mixing models responsible for estimating proportional contributions. Nevertheless, stable isotopes enable insights into consumer–resource relationships that would otherwise be difficult to impossible to quantify.

2.4 | Focus of the study

We focused on determining the importance of seagrasses, mangroves and tidal marshes to fish production; however, several other estuarine producers (epiphytes, algae, phytoplankton benthic organic material etc.) also contribute to fish diet. Such producers were often included in stable isotope studies we used in our analysis; however, the identity of which other producers were sampled varied greatly between individual studies hindering the ability to summarize them as extensively as seagrass, mangrove and tidal marsh ecosystem (see Appendix S2). However, these other producers were included in the calculation when normalizing fish-specific proportional contributions of ecosystems. Manuscript literature review raw data can be found in Appendix S2 and it can be updated when new ecosystem–fish isotope studies are published from Australia or it can be used as a cornerstone for other similar studies in the future.

Proportional contributions of each ecosystem type were summarized separately for each individual Australian state: Western Australia, South Australia, Victoria, New South Wales and Queensland. This is because fisheries in Australia are managed individually within each state. All statistical analyses for proportional contributions were carried out with tidyverse package (Wickham, 2017) in R version 3.4.3. (R Core Team, 2017). Boxplots were used to visualize ecosystem contributions to fish production (%) across Australian states. R code for calculating and visualizing proportional contributions as well as following economic analysis is available on request.

2.5 | Economic valuation

First, we determined which species were of commercial importance from our data set by using publicly available Australian fisheries reports for Victoria (Department of Primary Industries, 2012), New South Wales (ABARE-BRS, 2010; Stewart, Hegarty, Young, Fowler, & Craig, 2015), South Australia (ABARE-BRS, 2010; PRISA, 2015) and

Queensland (Queensland Fisheries Summary, 2018). From the same reports, we extracted the most recent 3 years of commercial catch data and applied consumer price inflation (CPI) correction (Reserve Bank of Australia, n.d.) to fisheries-specific annual state-wide catch values. Doing so enabled correction for historic dollar estimates against inflation and captures variation in annual catch and dollar values. Focus was given to commercially important species, because it provides a clear link for assessing the gross value product based on market values of fish. We assume that the entire harvestable fish population benefitted from the ecosystems that they were related to as stable isotope analysis is in 99% of cases done on adults. By not incorporating estimates of recreational fisheries value, our estimated economic values of coastal ecosystems are conservative (all monetary values are expressed in Australian dollars (\$ AUD) throughout the manuscript).

We then applied proportional contributions of coastal ecosystems to Consumer Price Index (CPI)-corrected average annual fish-specific catch values and estimated gross value product (GVP) of coastal ecosystems in monetary units. In economics, GVP can be defined as a measure of total economic activity in the production of new goods and services in an accounting period (see e.g., Colander, 2014). The calculations outlined below explain how species-specific proportional contributions were combined with CPI-corrected annual catch values to calculate an average GVP of coastal ecosystems and estimate standard deviations:

$$GVP_{l,p,s} = C_{l,p,s} \times AACV_{l,s}$$

where $GVP_{l,p,s}$ is the average gross value product (GVP) of ecosystems p derived from commercially harvested fish species s at location l , $C_{l,p,s}$ is the average contribution (C) of ecosystem p to consumer species s at location l , and $AACV_{l,s}$ is the average annual catch value for fish species s at location l . Standard deviations for $GVP_{l,p,s}$ were calculated with the following formula:

$$GVP_{l,p,s}SD = \sqrt{\frac{\sum (AVL_{l,s,n} - AACV_{l,s})^2}{n_s}}$$

where $GVP_{l,p,s}SD$ is the standard deviation of the gross value output of ecosystem; p is derived from commercially harvested fish species s at location l , $AVL_{l,s}$ is annual catch value for fish species s at location l , $AACV_{l,s}$ is the average annual catch value for fish species s at location l at year n and n_s is total number of annual catch values for species s at location l .

3 | RESULTS

3.1 | Proportional contributions

Seagrasses displayed the highest median proportional contributions to fish production across all studied Australian states (Figure 3). Mangroves and tidal marshes in Victoria and South Australia showed relatively minor proportional contributions (approximately 4%–5%) to fish production; however, proportional contributions of mangroves and tidal marshes increased in Queensland and New South Wales (Figure 3).

3.2 | Economic valuation

Across Australian states, 96 fish species of commercial relevance with an average annual catch of 49,000 tonnes (t) were supported by seagrass mangrove and tidal marsh ecosystems based on the stable isotope information. This estimation is based on the trophic energy flow. Average annual gross value product of seagrasses, mangroves and tidal marshes in Australia (excluding Northern Territory, Tasmania and Western Australia) was estimated to be 80 million Australian dollars (M AUD per year; Table 1, Figure 4). Forty-one per cent (20 t) of the average annual catch of commercially relevant fish was attributable to seagrass, mangrove and tidal marsh ecosystems based on fish-specific proportional contributions. Both tidal marshes and seagrasses were equally valued at 31.5 M AUD per year (39.4%) and mangroves at 14.9 M AUD per year (18.6%) (Table 1, Figure 4). Tidal marshes were the highest valued ecosystems in New South Wales (14.3 M AUD per year) and Queensland (16.5 M AUD per year; Table 1, Figure 4). Seagrasses were the highest valued ecosystem in South Australia (6.6 M AUD per year) and Victoria (1.9 M AUD per year);

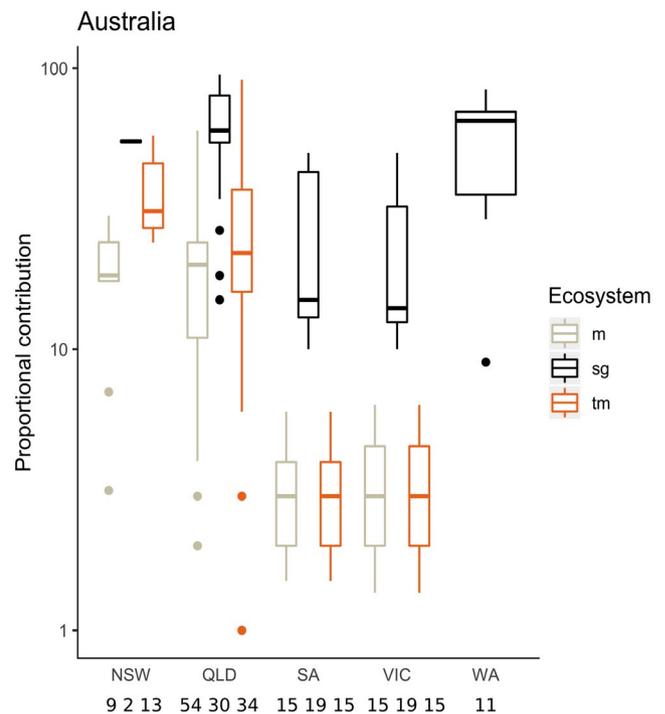


FIGURE 3 Proportional contributions of mangroves (m), seagrasses (sg) and tidal marshes (tm) to fish production in five Australian states (NSW, New South Wales; QLD, Queensland; SA, South Australia; VIC, Victoria; WA, Western Australia). Stable isotope studies in WA have only focussed on seagrass ecosystems; thus, no information about proportional contributions of mangroves and saltmarshes is present for WA. Numbers underneath each state show the number of individual fish species associated with each ecosystem. Solid line in the middle of the box represents the median, and the box itself represents interquartile range (IQR) which shows where 50% of the data is distributed. The lower and upper boundaries of the box represent 25th and 75th percentile. For the ease of plotting, y-scale has been displayed on log-scale [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Annual catch in tonnes (t/year) and value (AUD/year) distributable to coastal ecosystems based on fish-specific proportional contributions together with an average annual gross value production of seagrass, mangrove and tidal marsh ecosystems across Australia and in four Australian states (NSW, New South Wales; QLD, Queensland; SA, South Australia; VIC, Victoria)

Ecosystem and location	Catch (t/year)	M AUD per year	Area/ha	AUD ha ⁻¹ year ⁻¹
Australia (excl. NT, TAS, WA)				
SG	3,727	31.5	451,848	13.8
M	2,157	14.9	2,283,289	33
TM	4,159	31.5	981,947	32.1
NSW				
SG	842	12.9	23,850	539.8
M	1,084	5.8	16,651	350
TM	2,145	14.3	13,225	1,082
VIC				
SG	212	1.9	48,207	39
M	36	0.3	5,672	54.4
TM	36.5	0.3	43,457	7.1
QLD				
SG	2,065	10.1	1,582,719	6.4
M	1,002	8.4	419,694	20
TM	1,940	16.5	892,960	18.4
SA				
SG	608	6.6	628,513	10.6
M	35	0.4	9,831	43.8
TM	36	0.3	32,305	14.2

Note: Australian states such as NT, Northern Territory; Tas, Tasmania and WA, Western Australia were not included in the analysis due to the lack of data. Values marked in bold indicate ecosystems with the largest gross value production across Australia and within each state. Data layers for area estimates (ha⁻¹) were derived from seamapaaustralia.org.

however, they contributed significant 10 and 12.8 M AUD per year in Queensland and New South Wales, respectively (Table 1, Figure 4).

The highest annual per hectare dollar values of coastal ecosystems were assigned to ecosystems in New South Wales where tidal marshes were the highest valued ecosystems (1,083 AUD) followed by seagrasses (540 AUD) and mangroves (350 AUD). The highest fisheries-specific ecosystem values mainly originated from prawns and crabs (e.g., eastern king prawn (*Melicertus plebejus*) and the giant mud crab *Scylla serrata*) but fish such as mullets and whittings also provided a significant contribution (Table 2). A full list of 45 economically important species and subsequent values of coastal ecosystems can be found in Appendix S1.

4 | DISCUSSION

In this study, we collated and quantified proportional contributions of coastal ecosystems to fish and invertebrates across

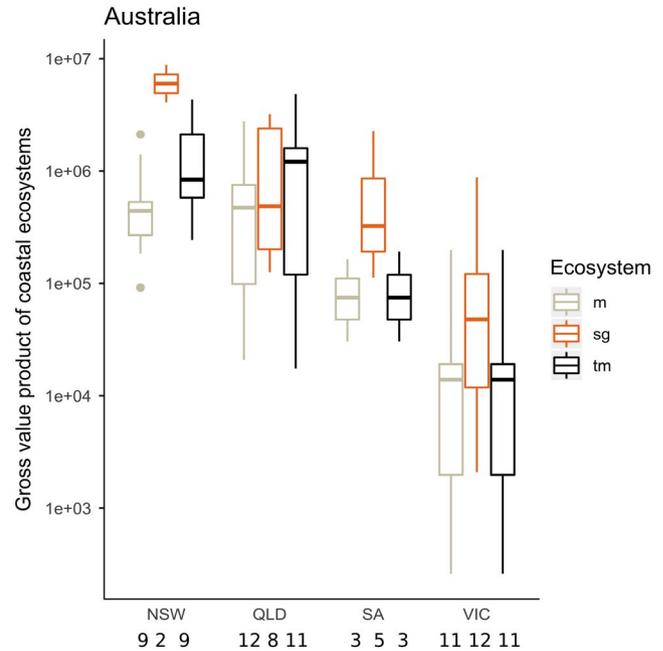


FIGURE 4 Annual gross value product in millions (M AUD per year) of mangroves (m), seagrasses (sg) and tidal marshes (tm) to fish production in four Australian states (NSW, New South Wales, QLD, Queensland, SA, South Australia, VIC, Victoria). Numbers underneath each state show the number of individual fish species associated with each ecosystem. Solid line in the middle of the box represents the median, and the box itself represents interquartile range (IQR) which shows where 50% of the data is distributed. The lower and upper boundaries of the box represent 25th and 75th percentile. For the ease of plotting, y-scale has been displayed on log-scale [Colour figure can be viewed at wileyonlinelibrary.com]

Australia. We evaluated patterns in ecosystem contributions to fisheries production and used these data to provide the first continental estimates of the economic value of coastal ecosystems using stable isotopes. Seagrasses consistently displayed the highest median proportional contributions to fish production across all studied states, whereas the input from mangroves and tidal marshes was highly variable. However, because of the contribution from tidal marshes to a number of highly valuable fisheries (prawns and crab), both tidal marshes and seagrasses were equally valued ecosystems (31.5 M AUD per year) followed by mangroves (14.9 M AUD per year).

While our estimated ecological and economic values of coastal ecosystems seem substantial across Australia, we still believe these estimates to be an underestimation. Firstly, the amount of fish species that have been sampled with stable isotope analysis only form a small fraction of the total species living in Australian coastal waters. Secondly, commercially important species in our data set also form only a small fraction of the total amount of species targeted by commercial fishermen, which leads to undervaluation of coastal ecosystems and services they provide. Also, we have not incorporated any value measures from recreational fisheries due to the scarcity of estimated catch from recreational

TABLE 2 Fisheries-specific average annual gross value production in million Australian dollars per year (M AUD per year) of coastal ecosystems

Species	State	Average annual catch				
		value	Catch (t)	Mangrove	Seagrass	Tidal marsh
Eastern king prawn (<i>Melicertus plebejus</i>)	NSW	13.6	560	0.5	8.8	4.3
Giant mud crab (<i>Scylla serrata</i>)	QLD	9.1	551	1.1	3.2	4.8
Tiger prawn (<i>Penaeus esculentus</i>)	QLD	7.2	456	2.8	4.5	
School prawn (<i>Metapenaeus macleayi</i>)	NSW	6.7	793	0.5	4.1	2.1
Sea mullet (<i>Mugil cephalus</i>)	NSW	6.1	1,980	2.1		4.0
Mulletts* (7 species grouped)	QLD	4.6	1,757	0.7	2.7	1.2
Whittings* (5 species grouped)	QLD	4.3	1,086	0.4	2.3	1.6
Blue swimmer crab (<i>Portunus armatus</i>)	SA	3.4	334	0.2	3.0	0.2
Barramundi (<i>Lates calcarifer</i>)	QLD	3.4	354	1.7		1.6
Banana shrimp (<i>Penaeus merguensis</i>)	QLD	3	356	0.6	0.8	1.6

Note: Species marked with * mean that catch data from Queensland fisheries reports did not differentiate between, for example various mullet or whiting species and provided an overall annual value for the fished group. However, our data set contained information about proportional contributions of coastal ecosystems for seven different mullet and five different whiting species. Thus, in this instance we pooled together and averaged proportional contributions of six mullet and five whiting species. Values marked in bold show the highest valued ecosystems for each commercially harvested species. Table has been ordered by species-specific average annual catch value (highest to lowest).

fisheries (see more about recreational fisheries below, under “Future directions”). Thirdly, we are lacking stable isotope information from Northern Territory, northern Western Australia and Tasmania, preventing us from calculating the economic values for coastal ecosystem in these regions.

To the best of our understanding, no other studies have been done elsewhere than Australia that combine stable isotopes with economic fisheries data. An average total economic output (from fisheries harvest) of tidal marshes and mangroves in Clarence river to be 25,741 and 5,297 AUD ha⁻¹ year⁻¹, respectively (Taylor et al., 2018), whereas an average total economic output in the Hunter River was 2,579 and 316 AUD ha⁻¹ year⁻¹ for tidal marsh and mangrove ecosystems, respectively (Taylor et al., 2018). In this study, researchers investigated two estuarine systems in northern New South Wales and linked proportional contributions of mangroves and tidal marshes to fish catch and value within each estuary. Calculated monetary estimates were then applied to overall ecosystem area within each estuary to estimate an average annual value per hectare of ecosystem. The main difference between our study and the work by Taylor et al. (2018) is in the scale of which proportional contributions of coastal ecosystems were linked to fisheries. Also, no ha⁻¹ year⁻¹ estimate from our data set reached dollar values as high as 2000 AUD. The Hunter River has no seagrass present, and to some degree, this may inflate the value of mangrove and saltmarsh habitats for this assessment when compared to estuaries where other producers are better represented (e.g., seagrass and *Phragmites*). The Clarence River also has little or no seagrass present, and may produce similar patterns. Or there is a possibility that fish species selected for the analysis simply have strong relationships with mangroves and tidal marshes and also have high market values (e.g., mud crab and blue swimmer crab) resulting in large economic values per hectare of ecosystem.

4.1 | Patterns across states

Proportional contributions of coastal ecosystems to fisheries production displayed notable variation across states (Figure 3). For example, seagrasses showed consistently higher median proportional contributions to fish production compared with mangroves and tidal marshes. This might be due to the fact that fish can more readily enter seagrass ecosystems as they are located in the intertidal or subtidal zones. Australia also possesses the greatest extent and one of the most diverse seagrass communities globally (Butler, Jernakoff, & Entry, 1999; Short, Carruthers, Dennison, & Waycott, 2007). Thus, it is likely that such a vast area of underwater primary producers translates into fish production. Fish can then uptake nutrition from seagrasses either by directly eating seagrass or indirectly through consumption of other smaller animals that derive their nutritional input from seagrasses. Higher proportional contributions of seagrasses might be also related to the possible difficulties of stable isotope mixing models to separate sources. Stable isotope values of saltmarshes can be less very similar to common species of seagrass (Raoult et al., 2018). Therefore, the absolute contribution of each ecosystem might be uncertain in areas where ecosystems that are tricky to separate are co-occurring; however, the combined contribution of these ecosystems is unlikely to vary. This issue may be overcome by analysis of a third tracer such as sulphur ($\delta^{34}\text{S}$; Connolly et al., 2004), although analysis of $\delta^{34}\text{S}$ is considerably more expensive than $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ which may limit its application.

Tidal marshes in Australia are located high in the intertidal zone and are infrequently inundated (Hollingsworth & Connolly, 2006); thus, aquatic species have very limited access to tidal marshes and in majority of the cases need to rely on transported organic material from these ecosystems (Melville & Connolly, 2005). Tidal marshes, however, have shown to provide a significant nutritional input to

prawn production in Australia (Raoult et al., 2018). This indicates that tidal marshes are able to export large amounts of organic material for invertebrates and fish in the food web. As a result, it is possible to value tidal marshes to fisheries from the perspective of energy transfer; however, stable isotope contributions ignore other ecological values such as the nursery value, or the predatory refuge. In this regard, Australian tidal marshes are unlikely to have, and thus, focusing on stable isotope contributions alone could overvalue tidal marsh and undervalue seagrass and mangroves. This highlights the need for a holistic fisheries valuation framework that considers both the food and habitat contributions (Taylor et al., 2018).

Several studies have found relatively little contribution of mangroves to food webs beyond their forest boundary due to the low nutritional content of mangrove leaves (Connolly & Waltham, 2015; Mazumder & Saintilan, 2010). However, organic mangrove particles in the range of >0.45 to <1,000 μm that get deposited on the seabed become part of fine benthic organic matter which has been identified as an important food source for several estuarine fish species by using stable isotopes (Hindell & Jenkins, 2004). Thus, the benefits of stable isotope analysis are further reflected by its ability to value areas in which fish do not physically occur or where they depend on organic material transported from nearby ecosystems (Raoult et al., 2018). Further, wider incorporation of sulphur stable isotopes could potentially provide an even better insight to mangrove particulates in the sediment. This is because sulphur-depleted mangrove sediments are likely to have very different signatures to other non-detrital pathways (Fry, Scalan, Winters, & Parker, 1982).

Furthermore, mangrove forests located throughout the southern coast of Australia (encompassing Victoria and South Australia) represent the southernmost distribution of mangroves in the world. Mangroves living close to their physiological tolerances are not growing as well as their tropical counterparts, and they resemble more shrub-like structures than an actual forest. For example, *Avicennia marina* along the southern coast of Australia reaches maximum height around 4–5 m, whereas 2,000 km further north in northern New South Wales or Queensland, the same species can grow up to 15–20 m and form dense forests (Australian National Botanic Gardens Centre for Australian National Biodiversity, n.d). Such a striking structural difference between mangroves likely affects their functional role in an ecosystem from a state-wide perspective. This might explain why we see an increase in proportional contributions of mangroves to fish production in warmer regions of Australia.

Differences in proportional contributions of ecosystems can be further affected by the extent of ecosystem area in each state (i.e., how much seagrass vs. mangrove, vs. tidal marsh). For example, the extent of mangroves and tidal marshes is greater in Queensland and New South Wales compared with Victoria and South Australia. In Queensland and New South Wales, combined mangroves, seagrass and tidal marsh represent 15%, 54% and 30% of the total ecosystem area and contribute 19%, 58% and 32% of diet based on stable isotopes. In comparison, in Victoria and South Australia combined mangroves, seagrass and tidal marsh represent 2%, 88% and 10% of the total ecosystem area and contribute 4%, 29% and 4% of diet.

4.2 | Assumptions and limitations

The basic concept behind data synthesis, reviews and meta-analysis is that there is a general 'truth' behind all conceptually similar scientific studies measured with a certain degree of error within individual studies (i.e., proportional ecosystem contributions). The aim is to use simple approaches to derive pooled estimates closest to the common unknown truth based on the conceptual similarities of data (Hillebrand & Gurevitch, 2016; Zlowodzki, Poolman, Kerkhoffs, Tornetta, & Bhandari, 2007). In principle, all existing methods should yield a weighted average from the results of individual studies; however, the way these weights are allocated and the way the uncertainty is computed varies or sometimes is not addressed at all (Gurevitch, Koricheva, Nakagawa, & Stewart, 2018). However, when performing a meta-analysis, a researcher has to make difficult choices that likely affect the results of the study. For example, how to best define objective criteria for selecting studies, aggregate variables, deal with incomplete data or how to best analyse and address uncertainty to name a few. Thus, we believe it is reasonable to point out various assumptions and areas of uncertainty ingrained in the approach, both to properly understand factors that affect the confidence in our estimates and also to provide guidance for future investigations around the same topic.

Proportional contributions of coastal ecosystems to fish production were summarized separately for each Australian state as fisheries in Australia are managed individually within each state. By doing so we assume that proportional contributions derived from regional studies appropriately reflect biological interactions and can be up-scaled for state-wide estimates. However, estuaries may differ in terms of their structural settings (e.g., slope of the shoreline, opening of the estuary mouth, current speed and flow within the estuary, size of the estuary) and abiotic variables (e.g., salinity levels, surface seawater temperature, nutrient levels and tidal range) that could impact the extent to which coastal ecosystems support fish production at each individual estuary (Taylor, Fry, Becker, & Moltschanivskyj, 2017).

During data extraction process, we pooled together mean and median proportional contributions of coastal ecosystems as there are no clear ways to estimate median values from means or vice versa. This likely creates a layer of uncertainty in our study when comparing the importance of proportional contributions to fish production across states and using proportional contributions in the subsequent economic analysis. This is because single extreme values in a data set can lead to high mean values whereas medians better reflect the distribution of data. To account for this variability, proportional contributions of coastal ecosystems to fish production that were sampled several times within the same state were averaged across studies. Also, when estimating macroaggregates or total values over large spatial scales, then higher level of variability within the data is acceptable compared with region-specific studies (Costanza et al., 2014).

Bias could also be present within individual studies incorporated into this review that likely affect the outcome and interpretation of

proportional contributions of coastal ecosystems to fish production. For example, it is often hard to differentiate SI signatures between ecologically similar species which might arise when species are either carbon enriched or depleted (Connolly, 2003; Connolly & Waltham, 2015; Melville & Connolly, 2005). If SI signatures of wider array of ecologically similar species can be successfully differentiated, then the analysis will result in a more robust outcome compared to a situation when focus is only on a few coastal ecosystems. Being able to differentiate between several ecosystems helps to minimize the possibility to overestimate the nutritional importance of any single ecosystem. However, Doughboy Creek and Annandale wetland in northern Queensland have mangrove- and saltmarsh-dominated areas (Abrantes & Sheaves, 2008, 2009; Creighton et al., 2017) and sampling in such environments results in accurate estimations of proportional contributions in instances when one type of ecosystem is present and the other is not. Otherwise, challenging discriminations between seagrass, mangrove and tidal marsh sources are then minimized when ecosystems are not co-occurring in a given space and time.

4.3 | Future directions

During economic valuation of coastal ecosystems, focus was given to use commercially important species; however, revenue created by the recreational fisheries sector is expected to be several times greater in various parts of Australia (Ford & Gilmour, 2013). This is because recreational fisheries inherently incorporate several indirect costs associated with fishing (e.g., licences, equipment, money spent on travelling). However, there is currently a significant lack of recreational fisheries catch data as well as fisher-specific information about these indirect costs. Unified framework for data collection is required before valuing ecosystem contribution to recreational fisheries over large spatial scales becomes viable. For now, focussing on commercially relevant species allows us to use annual state-wide fisheries reports and derive species-specific value estimates for coastal ecosystems and compare states to one another. There is a great deal of overlap between commercially and recreationally targeted species meaning that summarized proportional stable isotope contributions from this study can be combined with recreational catch information when it becomes more readily available in the future. Consideration of recreational harvest and other ecosystem services would result in more holistic valuation, but also increase the number of underlying assumptions which might rely on relationships that are more difficult to quantify.

Another potential future avenue for stable isotope fisheries research should focus more on complete sampling of fish throughout various life stages (e.g., recruits, juveniles and adults) to identify when species start first receiving nutritional input from coastal ecosystems (Carseldine & Tibbetts, 2005). As a result, it would be possible to highlight when/if dietary switches occur and how fish depend on different ecosystems at different stages of their lifecycle. Such information is important to fisheries managers for better understanding spatiotemporal dynamics between fish populations and coastal ecosystems.

The current ecological and economic valuation within this manuscript lacks input data from the Northern Territory, Tasmania and Western Australia. More stable isotope studies to derive proportional contributions of coastal ecosystems for the major fisheries in these regions are required to incorporate them into the national value estimations. However, total combined annual wild capture fisheries value from these three states was estimated at 430 million Australian dollars in 2009 (ABARE-BRS, 2010). This effectively highlights existing knowledge gaps and areas with imminent need for further research as all three states have fully functioning and economically important fisheries sector.

5 | CONCLUSIONS

We were able to value the contribution of coastal ecosystems to fisheries at a continental scale by, synthesizing existing food web/stable isotope studies and combining the outcome with a simple economic analysis. Doing so helps to reduce existing knowledge gaps and provides a significant contribution to current realm of Ecosystem Service delivery framework. This was achieved by outlining linkages between ecosystem production and demand on spatially relevant measures across one continent in a novel manner. Seagrasses were shown to be the most important ecosystems to fisheries production across Australia in terms of ecological importance (highest median proportional contributions) whereas tidal marshes and seagrasses both contributed equally (31.5 M AUD per year). The ecological importance of mangroves and tidal marshes was small on the southern (temperate) coast of Australia but increased in north-east (tropical) Australia. The highest fisheries-specific dollar values of seagrasses, mangroves and tidal marshes originated from prawns and crabs that are highly valued and commercially targeted species.

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DATA AVAILABILITY STATEMENT

All required data are accessible in Appendix S2.

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SUPPORTING INFORMATION

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

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