RESEARCH ARTICLE

Estimating enhanced fish production on restored shellfish reefs using automated data collection from underwater videos

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Abstract

1. Shellfish reefs across the world have been heavily degraded by mechanical harvesting, disease and declining water quality. In southern Australia, where substantial losses have occurred, government and non-government efforts to restore functioning reefs are now underway with a strong focus on enhancing fish productivity. However, the capacity of these restored reefs to enhance fish production remains unknown, hampering estimates of return on investment.

2. We quantify the density differences of newly recruited juvenile fish and other nekton on these restored reefs, relative to those on unrestored, unstructured habitat. Fish were surveyed at three paired reef-unstructured locations using 169 unbaited stereo video deployments during three periods over 12 months (2022–2023). We used automation software, FishID, to automatically identify, size and count fish in videos. We subsequently applied known growth and mortality parameters to model enhancement of fish productivity.

3. Sixteen species occurred as new recruits, with all but two found at higher densities on reefs than unstructured habitat. Enhancement of fish production from subtidal restored shellfish reefs from a single year's cohort is estimated to be, on average, $6186\,kg\,ha^{-1}\,year^{-1}$ (SD 1802) after enough time has elapsed for all species to have matured. Species harvested commercially or recreationally contributed 98% of that production ($6083\,kg\,ha^{-1}\,year^{-1}$, SD 1797).

4. Enhancement varied greatly among locations, ranging from $12{,}738\,kg\,ha^{-1}\,year^{-1}$ (SD 2894), which is the highest yet recorded anywhere, to $1.4\,kg\,ha^{-1}\,year^{-1}$ (SD 0.9).

5. The lack of juvenile fish at the location with the lowest estimated enhancement might be explained by the impact of overfishing on recruitment of key species or by an abundance of alternative habitat for juvenile fish.

6. *Synthesis and applications*. The combination of underwater videos with automated data extraction provides a reliable, cost-effective method for surveying fish on oyster reefs. By quantifying enhanced fish productivity on reefs, we provide estimates that will underpin calculations of ecological, social and financial benefits, supporting the business case for scaling-up restoration efforts.

KEYWORDS

artificial intelligence, *Chrysophrys auratus*, computer vision, great southern reef, marine habitat restoration

1 | INTRODUCTION

Shellfish reefs provide important ecosystem benefits including food and habitat provision, water filtration and shoreline protection (Coen et al., 2007; La Peyre et al., 2014; Meyer & Townsend, 2000; Ray & Fulweiler, 2021). Unfortunately, shellfish reefs have been almost extirpated globally, through a combination of overharvesting, declining water quality, disease and coastal development (Beck et al., 2011; Gillies et al., 2018; McAfee & Connell, 2021). In response to this loss of habitat and the benefits they provide, substantial efforts have been made to restore shellfish reefs, particularly oyster-dominated reefs (Howie & Bishop, 2021; McAfee et al., 2022). Many shellfish reef restoration projects identify enhancement of fish production as an objective (Hemraj et al., 2022). To quantify benefits from enhanced fish production, reliable estimates of newly recruited juveniles ('young of the year') on restored reefs and unrestored, unstructured habitat (i.e. the counterfactual to restoration) are needed. Traditional fish counting methods on reefs, such as nets and traps, disrupt fish behaviour and pose challenges on structurally complex reefs, especially with the need to sample a well-defined area of habitat. Recent developments in underwater cameras followed by automated extraction of fish sizes and counts from videos potentially provide a cost-effective solution that is unobtrusive to fish, can be deployed on structured and unstructured habitat and captures a lasting record (Connolly et al., 2021; Ditria et al., 2020; Marrable et al., 2022).

In the United States, where the majority of shellfish reef restoration programmes have occurred, there is extensive evidence that fish abundance is greater on restored reefs than on unrestored habitat, and that the higher abundance of juveniles on reefs can substantially enhance fish biomass (Zu Ermgassen et al., 2016). Similar reef restoration programmes are now underway along Australia's coastline, particularly in southern Australia, which was historically rich in shellfish reefs but experienced significant losses in the early 1900s (Gillies et al., 2018; McAfee & Connell, 2021; Schrobback et al., 2014). Since 2015, a major reef rebuilding programme has re-introduced subtidal structured habitats to the coastline, aiming to recover lost shellfish reefs and benefit biodiversity, including enhancing fish production in coastal seascapes (Gilby et al., 2021; McAfee et al., 2022; Oceans Program, 2021). However, the capacity of these restored reefs to enhance fish production remains uncertain, hampering the quantification of the benefits from restoration that ultimately drives the business case for scaling-up restoration efforts (Gillies et al., 2015).

The fisheries benefit of shellfish reefs manifests as direct use by adult fish, and increased survivorship of juvenile recruits, which ultimately contributes to enhanced fish biomass in the wider seascape (Peterson et al., 2003). The density of juvenile fish, specifically, is often also higher on restored reefs, and because of the limited availability of structured habitat for juvenile settlement along developed coastlines, this density differential is likely to lead to increased adult fish biomass in adjacent waters as fish migrate to other habitats ontogenetically (Nagelkerken et al., 2015). Total biomass enhancement estimates from traditional surveys of juveniles, and modelled using rates of growth and natural mortality for each fish species, range up to 6500 kg ha^{-1} year^{-1} (Zu Ermgassen et al., 2016, 2021). These biomass estimates are from the United States, predominantly from intertidal reefs or from an indistinguishable mix of intertidal and subtidal reefs. On restored shellfish reefs in Australia, there are no estimates of the long-term production of fish biomass nor estimates of juvenile densities, but there are reports of increased fish abundances. The numbers of fish on restored, subtidal reefs in southern Queensland are 16-fold greater than on adjacent unrestored habitats (Gilby et al., 2019), and are 10-fold higher than unstructured habitats on remnant intertidal reefs in New South Wales, averaged across seasons and locations (Martínez-Baena, 2022).

Here, we surveyed fish and other nekton species at three subtidal restored shellfish reefs across southern Australia, two in Victoria and one in South Australia. We surveyed both reef edge and reef interior, as there can be differences in fish use in these within-reef subhabitats (Hanke et al., 2017; Harwell et al., 2011). Fish were surveyed using unbaited stereo cameras at three times of the year to ensure that peak juvenile recruitment was captured for all species. Using automated software to identify, size and count animals, we compared juvenile densities between restored reefs and unstructured, unrestored habitat as the control habitat for restoration. The

increased densities on reefs were used to estimate enhanced biomass that would accrue as a result of restoration once all species had reached maturity, taking into account natural mortality (Peterson et al., 2003; Zu Ermgassen et al., 2021). We report substantial, but highly variable, biomass enhancement per unit area attributable to restoration.

2 | MATERIALS AND METHODS

2.1 | Survey region and reef description

The Nature Conservancy and partners have restored shellfish reefs at 13 locations across temperate Australia as part of a national shellfish reef restoration programme (Reef Builder) funded by the Australian Government and local agencies (Oceans Program, 2021). Three of the Reef Builder locations were selected for this study (Figure S1): Dromana (144.95162, −38.32655, restored in 2020–2021) and Margaret (144.94561, −37.89927, 2017–2021) in Port Phillip Bay, Victoria and Glenelg in Gulf St. Vincent, South Australia (138.49713, −34.96748, 2020–2021). All reefs comprised arrays of multiple reef units (from 0.01 to 0.06 ha and ranging 4.6–9.0 m in water depth), constructed using limestone rock and recycled shell as base material and seeded with spat of native flat oysters (*Ostrea angasi*) and blue mussels (*Mytilus planulatus/galloprovincialis*; Victoria only).

2.2 | Field survey methods

To quantify the fish biomass enhancement of restored reefs, we measured densities of 'young of the year' on reefs and adjacent unstructured habitat at each location. The control unstructured habitat was nearby soft-sediment seabed. No remnant reefs remain at or near the surveyed locations that could be used as positive reference sites. Reef and unstructured habitats in each

location were separated by 500–1000 m. Camera rigs within each habitat were separated by 20–200 m, with distances at the smaller end of that range being rigs at different ends of the same reef unit, providing enough separation to sample independently for these unbaited cameras. A total of 4–11 rigs were deployed on each habitat over 1–4 days depending on weather conditions (Table 1). To ensure that seasonal species were well represented and to maximise the chance of capturing peak juvenile recruitment for all species, surveys were conducted three times over the course of a year (Table 1). Reef and unstructured sites were sampled at the same time, between 09:00 and 14:00 h. Water depths were similar at reef and unstructured habitats (average reef and unstructured depths, respectively, were Dromana 7.28 and 7.09 m, Maragaret 8.58 and 8.93 m, Glenelg 6.15 and 6.08 m). Water clarity measured as the distance fish can be seen from each camera deployment (described below under 'Data extraction from videos') was also similar between reef and unstructured habitats (average reef and unstructured clarities, respectively, were Dromana 1.6 and 1.7 m, Maragaret 1.7 and 2.2 m, Glenelg 1.1 and 1.1 m). The locations are not strongly tidal and, in any case, any effect of tide is the same across habitats. Waters within locations are well mixed and no differences in water quality are expected between reef and unstructured habitats that could confound the effect of reef structure on fish (e.g. although water temperature changes seasonally, within a location the temperature over reef and unstructured habitats are within 1°C; Bureau of Meteorology, 2024). The reefs are not in protected waters and no permit was required to deploy cameras. Deployment of unbaited cameras was reviewed by Griffith University's Ethics Committee and no ethics approval was required.

Across all locations, we used 169 unbaited stereo Remote Underwater Video System (RUVs) deployments, each accommodating two Go Pro Hero 9 cameras positioned on a 30-cm baseline to optimise identification and sizing of small fish (Liu & Aggarwal, 2005; Santana-Garcon et al., 2014). Stereo-RUVs were calibrated ex situ by filming moving objects of known size underwater. Additional

TABLE 1 Timing and number of successful stereo video deployments per habitat and location across three survey periods.

Survey period & timing	Location	Number of days	Number of deployments per habitat			Total
			Reef edge	Reef flat	Unstructured	
1 May/June 2022	Dromana	4	10	11	7	28
	Margaret	2	11	7	8	26
	Glenelg	2	7	7	8	22
2 November/December 2022	Dromana	3	8	8	6	22
	Margaret	1	0	0	0	0
	Glenelg	2	6	5	6	17
3 March 2023	Dromana	1	6	6	6	18
	Margaret	2	8	8	10	26
	Glenelg	1	4	2	4	10
Total			60	54	55	169

Note: Extreme flooding near Margaret reduced water clarity and prevented deployments during survey period 2.

in situ ground-truths were done by filming objects of known size at the time of each deployment. Size estimates (described below) were within 10% of actual sizes (i.e. ±10% for 95% of objects). Stereo-RUVs were deployed randomly at each habitat and left to record for 1 h. On restored oyster reefs, divers positioned stereo-RUVs on top of the reef and at the edge (0.5 m from the edge of reef structure). The recorded period began once stereo-RUVs were on the seabed and divers had returned to the boat (Figure 1).

2.3 | Data extraction from videos

The first step in automating data extraction is to manually annotate images of nekton species (fish, cephalopods and swimming crabs, hereafter referred to as 'fish', following Australian fisheries guidelines (e.g. Fisheries Act, 1994)). Frames of identified species were annotated with bounding boxes using FishID software. We aimed for an equal number of annotations for each species, but ultimately some uncommon species had smaller numbers of annotations. As fish assemblages in Victoria and South Australia are different, annotation data were separated by state. Annotations from each state were further split into training, evaluation and testing data sets. Video preparation and image annotation took on average 43.6 h per survey period. Annotations were sourced from 11,443 frames, or 0.38% of total available frames. Training and evaluation data sets were used during training and optimization of a single shot detector (YOLOv5; Connolly et al., 2022). Testing data sets were used once for estimating detection model performance (performance estimates are based on F1 score, Precision and Recall). For preventing the likelihood of false negative and false positive at inference, we selected an optimal inference confidence threshold for each

species that balanced Precision and Recall (Mandal et al., 2018; Villon et al., 2020). Screening, annotation and detection model training procedures were repeated after each sampling event to avoid domain shift. Thus, detection models, one for each state, were updated for new species, or for an increased occurrence of species with low initial numbers of annotations.

For Victoria, the training data set contained 20,201 annotations of 25 species, with an additional 5996 annotations for evaluation. Testing on 5202 separate annotations showed that the model performed suitably well, with an average F1 score of 82% (Table S2). The performance for one class 'Monocanthidae', which consists of leatherjacket species that were too far from the camera to accurately identify to species level, underperformed relative to all other classes. Without this class, the average F1 score for Victoria was 85%. For a small number of rarer species, the number of images was limited and performance was poor, and therefore, detections for these species were manually curated and checked. For South Australia, fish were noticeably scarcer in all habitats. The model was trained with 5821 annotations, 1835 for evaluation and tested on 994 images, of 12 species, with very good accuracy (average F1 score of 95%). The performance of both models was on par with multispecies models reported for automated fish detection in other studies (Connolly et al., 2022; Villon et al., 2021). Once the models were finalised, all video deployments from each state were run through their respective detection model for prediction.

For each stereo deployment, we obtained fish detections on left and right cameras over the deployment duration (hereafter, detection timeline). Detections from the left camera were used to calculate relative abundance of fish per species. Mean Count rather than MaxN was used to provide a more accurate assessment of relative abundance (Conn, 2011; Ellis & DeMartini, 1995; Erickson
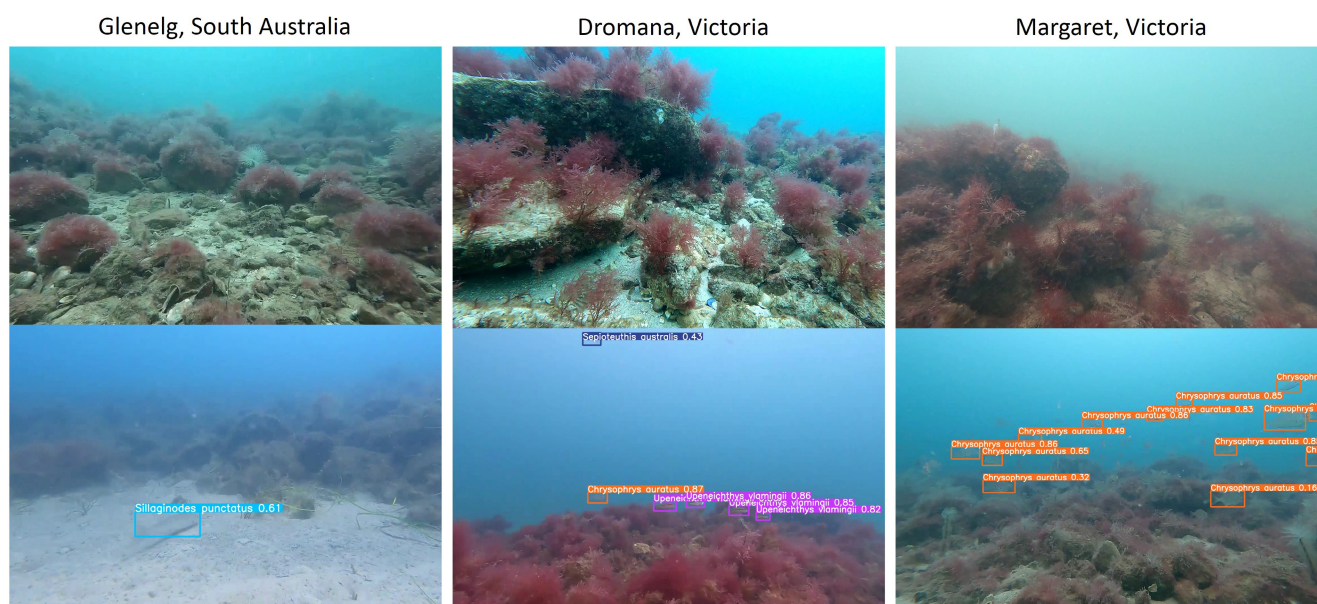

FIGURE 1 The three restored oyster reefs in southern Australia surveyed during the study (top row), and images showing fish identified and counted using FishID automated software (bottom row).

et al., 2023; Schobernd et al., 2014). Using the MaxN metric would have inflated recorded densities of juvenile fish in the known sample area by selecting only frames where the fish were most abundant in the field of view. Another strength of our data extraction procedure is having the estimate of sample area for each deployment, which allowed a more precise estimate of juvenile densities, both on reefs and unstructured control habitat. We filtered fish observations for each detection timeline, retaining a 1-min window of detections for every 5-min period for a maximum of 60 min (Figure S2), which best avoided over or underestimation. Filtered fish detections per species and video were averaged to produce a Mean Count.

Video clips from each camera (left and right) were synchronised and used to size fish (Sheaves et al., 2020). Sizing is a computer-intensive task, so we sized a fraction of all fish detected. For each deployment and species, we sized individuals in at least three frames (including the MaxN frame) for all cases where the species occurred with enough frequency to do so. Each frame selected for sizing was at least 10 min apart in the detection timeline to avoid pseudo replication of sizes. A total of 3341 individuals were sized, and we classified these as adults or juveniles based on life-history data collated via literature review (Table S1). Because we did not size fish in every frame used to estimate Mean Count, we estimated the proportion of juveniles occurring for each species in each deployment. We first created a size probability density function from observed sizes using a Kernel Density Estimation (KDE, Gaussian kernel with bandwidth 0.45). We evaluated the KDE at evenly spaced values between 0 and the maximum observed size for 1000 samples, and computed their probabilities from their log-likelihood values. Finally, we calculated the probability of the data falling below the juvenile size threshold. This juvenile probability per deployment and species was then applied to the Mean Count for that species to determine the proportion (and thus number) of juveniles per species per video.

The area over which juveniles were effectively identified and counted was determined by first assessing the distance between stereo RUVs and every individual sized. We then used the 90th percentile of the distance–frequency distribution per deployment and species as the maximum effective observable distance by our method. Thus, our approach takes into consideration variations in visibility and detectability across deployments and species, and assumes that some larger distance would occur beyond which juveniles typically could not be identified, counted or sized. We used camera geometry and the 90th distance percentiles (*distance*) for estimating the effective benthic habitat surveyed (approximated as a polynomial function, Equation 1). This area (*A*) was used to convert abundance counts to densities.

$$A = 5.0501 \times distance^2 - 13.058 \times distance + 9.0538. \quad (1)$$

2.4 | Modelling species-specific biomass enhancement

We estimated biomass enhancement on restored shellfish reefs following Zu Ermgassen et al. (2016). For each species, we calculated fish population density enhanced (*N*) by restored reefs at each location as:

$$N = d_{restored} - d_{control,} \quad (2)$$

where $d_{restored}$ is the average density of juvenile fish per hectare on a restored reef and $d_{control}$ is average density per hectare on an unstructured control. Only positive *N* values were used to estimate biomass enhancement. This assumes that abundant species at the unstructured control site are not habitat limited, unlike reef-dependant species. This assumption is framed upon the historical losses of shellfish reefs in southern Australia (Gillies et al., 2018). It is therefore assumed that the restoration of shellfish reefs would not negatively impact species that prefer unstructured habitats.

Variance of juvenile densities estimated from replicate sampling was averaged across paired restored and control sites (weighted by number of replicate samples) and then converted to standard error using the total number of replicates belonging to paired restored and control sites. The density of individuals enhanced by restoration and surviving through time (*t*) was calculated as:

$$\frac{dN}{dt} = -M_t N, \quad (3)$$

where M_t is the species' mortality rate and *N* is enhanced density from Equation (2). We assumed *M* is constant through time, meaning:

$$N_t = N_{0.5} e^{(-M \times (t-0.5))}, \quad (4)$$

where $N_{0.5}$ is density enhancement at 0.5 years (Equation 2). Length (cm) of individuals surviving in each year (N_t) was calculated using the von Bertalanffy growth equation:

$$L_t = L_\infty \left(1 - e^{(-K(t-t_0))}\right), \quad (5)$$

where L_∞ is the maximum length (cm) of the species, *K* is the species' Brody growth coefficient and t_0 is the theoretical length of the species at age 0. For all species except Southern squid (*Sepioteuthis australis*), known length–weight relationships were used to estimate individual weight (grams) in each year:

$$W_t = aL_t^{\,b}, \quad (6)$$

where *a* is the intercept and *b* is the slope of the length–weight relationship, and length (L_t) is from Equation (4). For Southern squid, weight was calculated using a known age–weight relationship (Pecl, 2004), substituting age (days) for length (L_t) in Equation (5). Net biomass enhancement was calculated as:

$$B_t = N_t (W_t - W_{t-1}), \quad (7)$$

where *t* is ≥ the time of maturity for that species (or for harvested species, time of recruitment to the fishery) and ≤ to maximum age, N_t is the density of surviving individuals from Equation (3) and W_t is weight from Equation (6). Net biomass enhancement was assumed to be at equilibrium when time (*t*) reached the maximum age for the species.

We propagated uncertainty in density enhancement estimates through to biomass enhancement by simulating the sampling

distribution of mean density enhancement values (*N*) given standard error estimated from replicate samples of paired restored and control sites. The sampling distribution was simulated by drawing 10,000 random values from a normal distribution truncated at 0, as fish density cannot be less than 0. Values drawn from the truncated normal distribution were scaled so that the final sampling distribution had a mean equivalent to the raw average density enhancement value (*N*) and a standard deviation equivalent to the standard error.

For species with sexual dimorphism influencing the value of life-history parameters relevant to Equations (2)–(7), we assumed a 1:1 male to female ratio, simulated density enhancement separately and summed the male and female biomass in each year to calculate the total for that species.

For each species at each location, the average and standard deviation of the 10,000 simulations in each year were taken to represent net biomass enhancement with uncertainty through time. When biomass enhancement was summed across all species to obtain a total, the variances of the net biomass enhancement for each species were also summed to produce the total standard deviation. We also assessed the sensitivity of model outcomes to mortality rates, as previous studies have found this to be an influential life-history parameter (Zu Ermgassen et al., 2016).

Assemblages of juvenile fish were compared between habitats (reef vs. unstructured) and among locations, using Permanova and a non-metric multidimensional scaling with Jaccard dissimilarity index (using R package 'vegan'; Oksanen et al., 2022) on species presence/absence.

3 | RESULTS

Across the three locations and habitat types, we identified 25 species (Table 2; excluding several species recorded as isolated instances, i.e. in <3 deployments over the whole study), 22 in Victoria, 10 in South Australia and 7 occurring in both. We found 16 species occurring as newly recruited juveniles, that is, 'young of the year' in Victoria, and of those, 2 occurred in South Australia (Table 2). Shannon diversity indices were greater for reefs than unstructured habitat at all locations (Table 2). Assemblages of juvenile fish differed most strongly among locations (Permanova: *p*=0.001). Assemblages at the two Victorian locations, Dromana and Margaret, overlapped,

but were distinct from those at Glenelg (Figure S4). The influence of habitat was significant (*p*=0.005) although secondary to location (Figure S4).

Densities of juveniles varied among species and among locations (Table 3). Densities in the two reef habitats, edge and flat, were not significantly different for any species (*t*-tests, all *p* values >0.05), and typical reefs are made up of clusters that contain edge and flat areas; therefore, we used the average of those habitats to estimate the density difference between reef and unstructured habitats for biomass calculations.

Enhancement of fish production is estimated to be, on average, 6186 kg ha^{-1} year^{-1} (SD 1802) by the time reefs have been in place long enough for all species to mature (Figure 2). Species harvested commercially or recreationally contributed 98% of that production (6083 kg ha^{-1} year^{-1}, SD 1797) (Figure 2). Enhancement varied greatly among locations (Figure 3), ranging from 12,738 kg ha^{-1} year^{-1} (SD 2895) at Margaret to 1.4 kg ha^{-1} year^{-1} (SD 0.9) at Glenelg. While southern hulafish (*Trachinops caudimaculatus*) were the most abundant juveniles at Margaret, they contributed little to biomass enhancement as it is a small, short-lived species. Juveniles of Australasian snapper (*Chrysophrys auratus*) were second most abundant, and, by contrast, this species is large and long-lived (maximum age 40 years), and dominated the total estimates of biomass. Other species contributing significant biomass were Australian herring (*Arripis georgianus*), velvet leatherjacket (*Meuschenia scaber*) and southern squid (*Sepioteuthis australis*), a cephalopod with an annual lifecycle for which juveniles were defined as being <125 mm mantle length, or about 100 days old (Pecl, 2000). We found the sensitivity of the model to mortality varied by species but not location, and that Australasian snapper, southern Maori wrasse (*Ophthalmolepis lineolatus*) and silver belly (*Parequula melbournensis*) biomass enhancement estimates were most sensitive (Figure S3).

4 | DISCUSSION

This study used automated video sampling to provide the first large-scale quantification of biomass enhancement of restored shellfish reefs in Australia. Previous work has reported higher fish abundance on restored reefs than on unrestored habitat (Gilby et al., 2021) as well as greater diversity and richness (Gilby et al., 2019, 2021). By

TABLE 2 Number of species recorded (any age), and number of species present as juveniles, for those with higher and lower densities on restored reef relative to unstructured habitat.

	Location	Total number of species	Number of species present as juveniles	Number of species with juvenile density greater on reef	Number of species with juvenile density greater in unstructured	Shannon diversity index (reef/unstructured)
Victoria	Dromana	22	14	13	1	1.7/0.8
	Margaret	22	12	11	1	1.1/0.1
South Australia	Glenelg	10	4	2	2	0.7/0.1

Note: Total species counts exclude several additional species recorded as isolated instances, i.e. <3 deployments over the whole study.

TABLE 3 Fish densities and estimated biomass enhancement, ordered by location and the amount of biomass enhancement.

Location	Common name	Species name	Family	Density reef (juveniles 100 m⁻²)		Density difference: Reef minus unstructured (juveniles 100 m⁻²)		Biomass enhancement at equilibrium (kg ha⁻¹ year⁻¹)	
				Edge	Flat	Mean	SD	Mean	SD
Dromana	Australasian snapper	*Chrysophrys auratus*	Sparidae	6.92	8	7.41	6.37	5497.42	1145.38
	Velvet leatherjacket	*Meuschenia scaber*	Monacanthidae	3.02	32.36	19.79	42.75	303.79	218.79
	Southern squid	*Sepioteuthis australis*	Loliginidae	0.7	2.65	1.67	3.36	13.61	6.28
	Silverbelly	*Parequula melbournensis*	Gerreidae	3.47	8.11	6.12	9.38	3.64	1.86
	Slender-spined porcupine fish	*Diodon nicthemerus*	Diodontidae	0.23	0.35	0.30	0.45	0.96	0.48
	Bridled leatherjacket	*Acanthaluteres spilomelanurus*	Monacanthidae	0.84	1.02	0.93	1.39	0.15	0.05
	Yellow-tailed scad	*Trachurus novaezelandiae*	Carangidae	<0.01	<0.01	<0.01	<0.01	0.09	0.05
	Little weed whiting	*Neoodax balteatus*	Odacidae	2.39	1.25	1.74	2.32	0.08	0.03
	Australian barracuda	*Sphyraena novaehollandiae*	Sphyraenidae	<0.01	<0.01	<0.01	<0.01	0.05	0.03
	Southern Maori wrasse	*Ophthalmolepis lineolatus*	Labridae	<0.01	<0.01	<0.01	<0.01	0.01	0.01
	Australian salmon	*Arripis trutta*	Arripidae	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
	Blue spotted goatfish	*Upeneichthys vlamingii*	Mullidae	<0.01	0.01	0.01	0.01	<0.01	<0.01
	Smooth toadfish	*Tetractenos glaber*	Tetraodontidae	0.05	0.01	0.03	0.05	<0.01	<0.01
	Total			17.62	53.76	35.69		5819.80	1166.12
Margaret	Australasian snapper	*Chrysophrys auratus*	Sparidae	13.57	22.68	17.11	19.91	12,686.78	2894.68
	Australian Herring	*Arripis georgianus*	Arripidae	2.66	1.28	1.97	6.35	37.56	19.12
	Southern Maori wrasse	*Ophthalmolepis lineolatus*	Labridae	0.08	1.62	0.68	1.61	12.58	5.88
	Southern hula fish	*Trachinops caudimaculatus*	Plesiopidae	4.75	35.51	20.13	56.79	0.37	0.16
	Little weed whiting	*Neoodax balteatus*	Odacidae	2.21	5.73	3.58	4.57	0.16	0.04
	Velvet leatherjacket	*Meuschenia scaber*	Monacanthidae	<0.01	<0.01	<0.01	0.01	0.04	0.03
	Slender-spined porcupine fish	*Diodon nicthemerus*	Diodontidae	0.01	<0.01	<0.01	0.02	0.01	0.01
	Southern garfish	*Hyporhamphus melanochir*	Hemiramphidae	0.06	<0.01	0.03	0.12	0.01	<0.01
	Blue spotted goatfish	*Upeneichthys vlamingii*	Mullidae	<0.01	<0.01	<0.01	0.01	<0.01	<0.01
	Bridled leatherjacket	*Acanthaluteres spilomelanurus*	Monacanthidae	0.04	<0.01	0.02	0.07	<0.01	<0.01
	Southern squid	*Sepioteuthis australis*	Loliginidae	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
	Total			23.38	66.82	45.10		12,737.50	2894.75
Glenelg	Southern squid	*Sepioteuthis australis*	Loliginidae	<0.01	0.32	0.17	0.43	1.41	0.86
	Blue spotted goatfish	*Upeneichthys vlamingii*	Mullidae	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
	Total			<0.01	0.32	0.17		1.41	0.86

Note: Juvenile fish density differences (reef – unstructured) shown for species more abundant on reef than unstructured (2 species less abundant on reefs not shown). Enhanced production estimated at equilibrium, that is, long enough for all species to reach their maximum age. Total densities and biomass enhancement per location represented as the sum of the values for each species within that location. Total SD for biomass enhancement per location is the square root of the sum of variances for each species. All biological parameters are in Table S1.
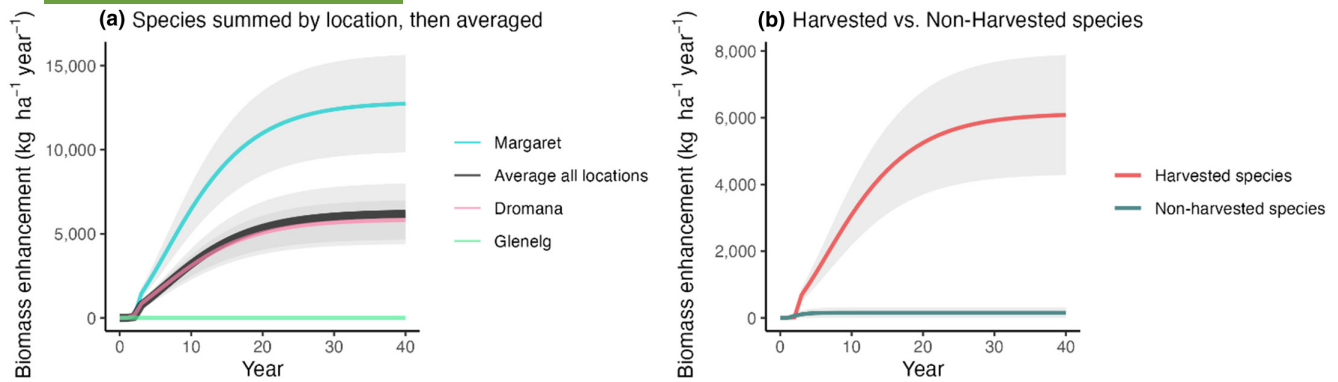
FIGURE 2 Biomass enhancement (mean ± SD) resulting from reef restoration in southern Australia, modelled for a single year's cohort of recruiting juveniles after enough time has elapsed for all species to mature (i.e. 40 years). (a) Biomass estimates for three locations across Victoria and South Australia, and the average of all locations. (b) Comparison of biomass enhancement attributable to species that are harvested (i.e. targeted commercially/recreationally) and not harvested.
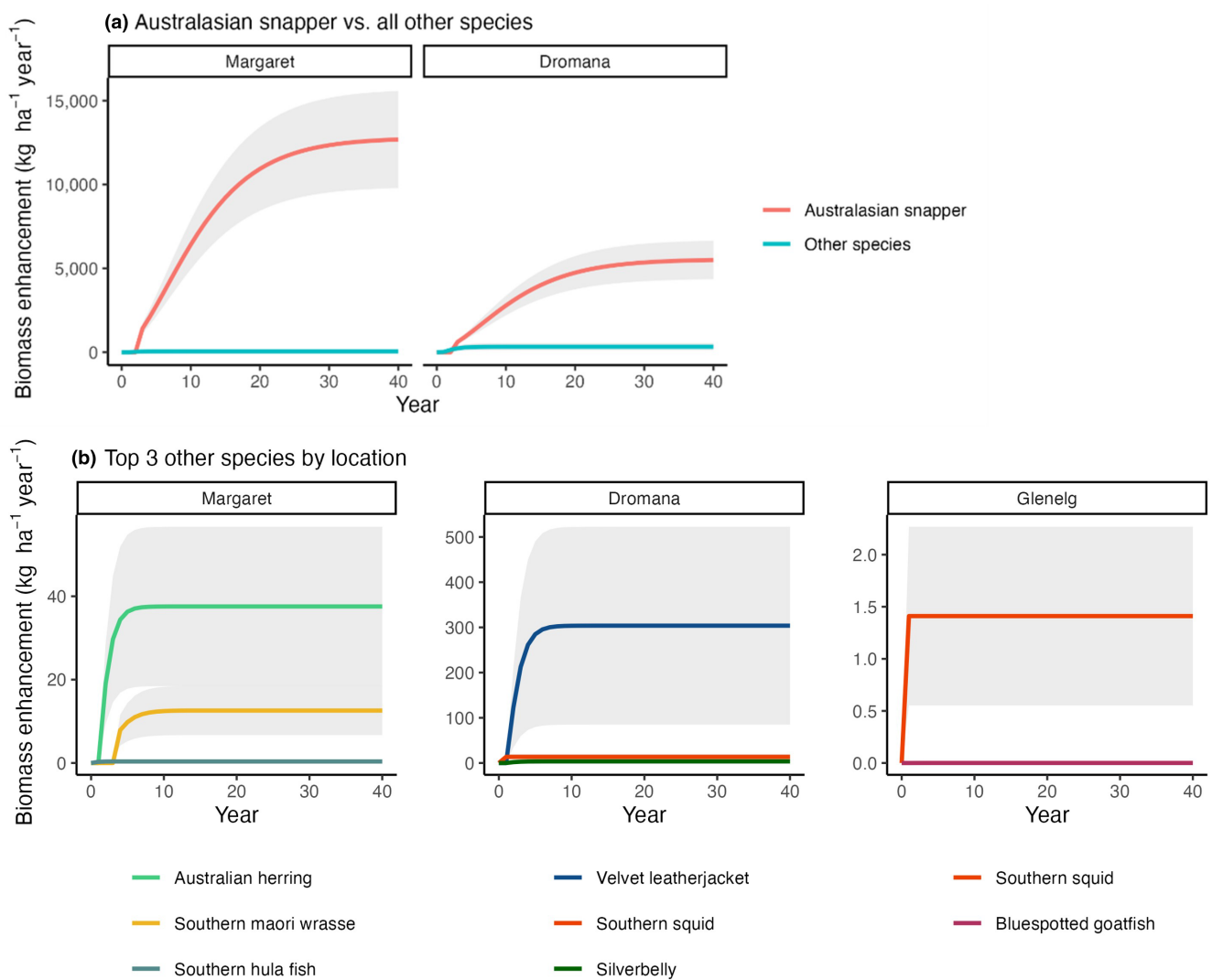

FIGURE 3 Biomass enhancement (mean ± SD) for the three locations in southern Australia, modelled for a single year's cohort after enough time has elapsed for all species to mature (i.e. 40 years). (a) Australasian snapper biomass versus all other species (Margaret and Dromana reefs only; no snapper juveniles at Glenelg). (b) Key species other than Australasian snapper (for list of all species, see Table 3). For Glenelg, only two species were enhanced by reefs. Given high variability in biomass enhancement across locations, y-axes vary by multiple orders of magnitude.

including size estimates, we were able to quantify the abundance of juveniles and thus estimate fish *production* as distinct from simple attraction of fish to restored reefs (Brickhill et al., 2005; Gilby et al., 2021), which enables potential future inclusion in environmental economic accounting and creation of natural capital accounts (e.g. the System of Environmental Economic Accounting; Edens et al., 2022). The biomass enhancement estimates for Victorian reefs are at the high end of previous estimates, all of which are from the United States (and acknowledging different fish survey methods of previous studies). Previous estimates of biomass enhancement at individual reefs of a similar size to those in the current study range from upper estimates of $1200 \, kg \, ha^{-1} year^{-1}$ (Humphries & La Peyre, 2015) and $1100 \, kg \, ha^{-1} year^{-1}$ (Stunz et al., 2010) to a low of $44 \, kg \, ha^{-1} year^{-1}$ (De Santiago et al., 2019). Meta-analyses estimating biomass enhancement from juvenile fish densities reported at several other locations provide summaries across the Gulf of Mexico and Atlantic coasts of United States, with values ranging from 2600 to $6500 \, kg \, ha^{-1} year^{-1}$ (Peterson et al., 2003; Zu Ermgassen et al., 2016, 2021). The estimate of biomass enhancement for Dromana, at $5800 \, kg \, ha^{-1} year^{-1}$, is clearly towards the high end of previously reported values, and the estimate of $12,700 \, kg \, ha^{-1} year^{-1}$ at Margaret is higher than any previous estimate. Conversely, there is no previous record of such a low biomass enhancement as the $2 \, kg \, ha^{-1} year^{-1}$ at Glenelg. These estimates of biomass enhancement are valuable as the first data for subtidal restored reefs in Australia.

Biomass enhancement at Victorian reefs was predominantly of species that are harvested commercially and/or recreationally (98%) and was dominated by a single species, Australasian snapper (*Chrysophrys auratus*). Harvested species are larger, and longer lived; therefore, juveniles produce more biomass over their lifetime. While our biomass estimates from two locations are high, since the majority of production was from Australasian snapper, a large, heavy and long-lived species (max ~130 cm, 17 kg, 40+ years; Moran & Burton, 1990), they are defensible. This quantitative dominance of biomass enhancement by a single species is very unusual. Typically, several key species comprise about 80% of the biomass; this is the case for all but one of the eight comparable studies of biomass enhancement from oyster reefs in the United States. The exception is the study by Humphries and La Peyre (2015) from a reef in Caillou Lake, Louisiana, where a smaller sparid fish, sheepshead (*Archosargus probatocephalus*), comprised nearly 80% of the enhanced biomass. The very high modelled production of Australasian snapper from restored reefs is reasonable in the context of the life history of the species in Port Phillip Bay. First, the species settles as juveniles onto structured habitat, the area of which has been substantially reduced over the last 150 years, so the new structure provided by restored oyster reefs was expected to be heavily utilised. This has been observed for juvenile snapper recruiting to restored mussel reefs in New Zealand (Sea et al., 2022). Second, the most recent assessment of annual catch of this species in Port Phillip Bay is in the order of 200 tonnes recreationally, and 80 tonnes commercially (via long-line licences; Ford & Gilmour, 2013; Bell et al., 2022). In Port Phillip Bay, the Reef Builder programme has to date restored oyster habitat with

a hard reef area of at least 1.32 ha (hard reef areas: Margaret 0.32 ha, Dromana 0.27 ha, other reefs 0.73 ha). Using our average estimated biomass enhancement for the bay of $9279 \, kg \, ha^{-1} year^{-1}$, the current restored reef structures are estimated to provide an overall biomass enhancement of $12,201 \, kg \, year^{-1}$ in the bay. Much of that would be due to Australasian snapper, and in the context of the current fishery for this species, the ultimate production of another 12 tonnes of harvestable biomass from a year's cohort of juveniles does seem possible. That harvestable biomass is estimated for unfished stocks (i.e. zero fishing mortality). The realised benefit of harvested biomass is likely to be less since fishing tends to target younger, smaller individuals, especially when harvesting pressure is high, thus limiting production from older, larger fish (Pauly et al., 1998). The relationship between the area of reef and the increase in fish production is unlikely to be linear, so as restoration efforts continue, estimates of biomass enhancement will have to account for this non-linearity of fish production from structured habitats; that is, the influence per unit area of hard structure decreases with increased availability.

Most of the additional fish production resulting from reef restoration is expected to enhance the surrounding seascape and not just the restored habitat itself (Coen et al., 2007; Grabowski & Peterson, 2007; Mann & Harding, 1997). For benthic species such as Australasian snapper, a range of habitats are utilised as fish move ontogenetically, linking the food webs of adjacent habitats in the seascape (Nagelkerken et al., 2015). Some of the benefits from juveniles are not evident by looking at biomass enhancement alone (Sheaves et al., 2015). For example, the species with highest on-reef abundance of juveniles at Margaret, southern hulafish (*Trachinops caudimaculatus*), is a small species (maximum length 15 cm) and contributed relatively little to biomass enhancement despite their numerical dominance. While hulafish themselves are not of commercial or recreational importance, as planktivores, their abundance on the reefs may indicate enhanced plankton productivity (Hunt et al., 2011). Temperate reefs are often regulated bottom-up with planktivorous fish supporting food webs as an abundant prey item for fish feeding at higher trophic levels (Frederikson et al., 2006; Martínez-Baena et al., 2023; Truong et al., 2017). Several other species abundant in this study are predominantly pelagic, such as Australian herring (*Arripus georgianus*), Australian salmon (*Arripus trutta*) and southern squid (*Sepioteuthis australis*). The presence of these species on the reefs as juveniles indicates a potentially important link between the benthic structure of reefs and the pelagic food webs of Australia's coastal seascapes, as has been noted elsewhere (Félix-Hackradt et al., 2014). Overall, we expect the contributions of juveniles on the restored reefs in Victoria to adjacent coastal habitats to be consistent with those previously reported for coastal and estuarine systems (Gilby et al., 2019; Grabowski et al., 2005). Further studies investigating pelagic survivorship post-recruitment, for example using chemical otolith markers (Elsdon et al., 2008; Shima & Swearer, 2016), will help to understand the degree to which shellfish reefs support and supply the wider seascape.

At the location in South Australia, juvenile fish were scarce and the estimate of biomass enhancement resulting from restoration

was therefore very small. There are several potential explanations for this lack of juvenile fish. For Australasian snapper specifically, this might be explained by the heavily overharvested fishery in Gulf St. Vincent (Cartwright et al., 2021), potentially indicating a fishery limited by egg production rather than settlement habitat (Fowler et al., 2021). This is contrary to the Australasian snapper fishery in Victoria where supply of juvenile fish is considered strong (Conron et al., 2020). For all species, there is the possibility that recruitment pulses of new settled juveniles might have been missed by our sampling because juveniles settled briefly and then left the reef between our three survey periods, or alternatively, the whole year had poor recruitment rates. Given interannual variability in the strength of recruitment for some of the key harvested species in South Australia (e.g. King George whiting; Rogers et al., 2021), and the influence of inter-annual weather patterns such as El Niño Southern Oscillation events (noting that 2022–2023 was a La Niña period), ongoing monitoring at this location will be especially important to ensure that our low estimate of biomass enhancement is not misleading. Other possible explanations for low juvenile fish abundance at the Glenelg reef are (1) differences in the physical properties of the systems, with Glenelg located in an open-water gulf while Dromana and Margaret are situated in a semi-enclosed protected bay and (2) a greater extent of alternative structured habitat such as seagrass in Gulf St. Vincent, compared to the patchy and much reduced extent of seagrass historically in Port Phillip Bay (Connolly et al., 2018), further supporting the above statement that the production at Glenelg may not be habitat limited and is instead subject to other bottlenecks, such as reduced egg supply. It is unlikely in this scenario that the age of the reef influenced juvenile densities, as Glenelg reef was constructed in the same years as Dromana (2020–2021; Margaret reef units installed between 2017 and 2020), and although some reef units at Glenelg are up to 5 years younger than at Margaret, other studies have shown that reef age is not an important variable in estimating the benefits of restoration (Hemraj et al., 2022). Although our focus is on fish production, restored oyster reefs also provide many other benefits that are valuable to consider in complement to fish production. For example, the Glenelg reefs have some of the highest oyster recruitment rates recorded on restored oyster reefs in southern Australia (S. Reeves, pers. obs. 2023), potentially provide habitat for adult fish and are expected to fulfil an important role in nutrient mitigation (Gillies et al., 2020). This emphasises that success for each restoration location should be considered in terms of the full suite of benefits (ecological, social and economic) rather than potential bias of singular elements alone.

The combination of stereo underwater cameras and automated data extraction from videos, followed by modelling based on growth and mortality rates, allowed us to estimate the biomass enhancement resulting from reef restoration. This is the first study to use video data to quantify biomass enhancement on restored shellfish reefs. Previous methods have involved physical capture of fish, for example, using fyke, block, gill and lift nets alongside reefs, or benthic sleds, traps or drop samplers either on reefs or alongside (Peterson et al., 2003; Tolley & Volety, 2005; Zu Ermgassen et al., 2016, 2021).

Remote underwater video systems (RUVs) are more commonly used in Australia than elsewhere (Lopez-Marcano, Brown, et al., 2021; Whitmarsh et al., 2017), and a small number of Australian studies of fish on oyster reefs have used them to monitor fish abundance (Gilby et al., 2019, 2021; Martínez-Baena et al., 2022). None of those studies estimated fish size and therefore could not estimate biomass enhancement. Nor have any studies of oyster reefs used automation to extract juvenile fish data from videos. Automated data extraction enabled good replication of stereo deployments across locations, in habitats that are challenging to survey quantitatively using traditional methods. It follows recent uses of automated video analysis from underwater cameras at restoration sites for other highly structured habitats such as mangrove forests (Kitchingman et al., 2023). It also allowed effective and consistent monitoring of the structured reef habitat and the unstructured, unrestored seabed using the same sampling method. The stereo cameras allowed successful identification and sizing of juvenile fish. The software automating fish identification, counts and sizes, performed well, with accuracy for individual species mostly between 80% and 100%. This is comparable to recent reports of multispecies models developed elsewhere, where F1 typically ranges from 73% to 92.3% (Ditria et al., 2020; Lopez-Marcano, Jinks, et al., 2021; Villon et al., 2021). Accuracy for Australasian snapper was lower (52%), mainly due to low recall, meaning that there was a relatively high rate of false negatives. This type of error underpredicts occurrences (Sheaves et al., 2020); therefore, the estimates for Australasian snapper could be considered underestimates rather than overestimates.

Beyond reporting reliable density estimates for fish, variability is introduced into estimates when using literature values for biological parameters. We prioritised the selection of growth and mortality data from literature specific to the species and location of interest; however, these rates vary through space and time, and some species were data deficient. This, at times, required averaging values from multiple sources, or calculating values based on known parameters (Table S1). Sensitivity analysis showed that mortality rate had a large influence on estimates for some species, including Australasian snapper where production estimates would be lower if mortality rates based on maximum age rather than on literature values were used (Figure S3). Region-specific uncertainty in other life-history parameters (e.g. growth and maturity) remains unknown for most species; therefore, these uncertainties could not be incorporated into the biomass enhancement modelling. However, due to the lack of data, not incorporating growth and maturity into models is standard practice for production estimates and has been identified as a caveat in other fish production studies (Zu Ermgassen et al., 2021). Unfortunately, until further analysis of species growth and mortality can be conducted within the regions of interest, this will remain a challenge for biomass enhancement modelling.

Automated analysis of underwater videos provided accurate density estimates by allowing us to use Mean Counts over a defined survey area for each deployment, all with reduced manual labour. The reported estimates of biomass enhancement for restored reefs can help to support natural capital accounting and assessments

of cost–benefit for shellfish restoration in southern Australia. Confidence in the biomass values will increase with future monitoring that refines estimates of inter-annual variability in the densities of juvenile fish. There is also scope for comparative studies of the effects of the position of restored reefs in the seascape (Gilby et al., 2018; Pittman et al., 2021; Vozzo et al., 2023), for example with proximity to other reefs and other structured habitats. Furthermore, at a smaller scale, the effects of structured habitats in coastal waters can alter fish densities just beyond the structure itself (Smith et al., 2008) in unstructured habitat abutting reefs. Fine-scale sampling of fish on soft-sediment habitat immediately adjacent to restored reefs is therefore warranted to further refine estimates of restoration benefits.

AUTHOR CONTRIBUTIONS

Rod M. Connolly, Craig D. H. Sherman, Christopher J. Brown and Simon E. Reeves conceived the ideas and designed methodology; Rod M. Connolly, Cesar Herrera, Jasmine Rasmussen, Kristin I. Jinks, Craig D. H. Sherman, Sebastian Lopez-Marcano, Ryan Baring and Brad Martin collected the data; Rod M. Connolly, Cesar Herrera, Jasmine Rasmussen, Christina A. Buelow, Michael Sievers, Kristin I. Jinks, Sebastian Lopez-Marcano, Francisco Martínez-Baena, Christopher J. Brown and Simon E. Reeves analysed the data; Rod M. Connolly, Cesar Herrera, Jasmine Rasmussen, Christina A. Buelow and Michael Sievers led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

None of the authors have conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from Dryad Digital Repository: https://doi.org/10.5061/dryad.9w0vt4bph (Connolly et al., 2024).

STATEMENT OF INCLUSION

Our study was led by the fish ecology team at Griffith University using their bespoke FishID software to automatically extract fish data from underwater videos, in collaboration with researchers from the organisation that restored the reefs, The Nature Conservancy and local researchers at each location who are authors or are listed in acknowledgements.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: Location and reef bathymetry for the three TNC restored shellfish reefs assessed in this study.

Figure S2: Variations in the relative abundance of two focal species, Australasian snapper (a solitary species) and leatherjackets (a sedentary species), as measured by meanCount, are depicted under different combinations of detection timelines, windows, and periods.

Figure S3: Sensitivity of biomass enhancement to mortality rates derived from the literature vs. those calculated using the species' maximum age.

Figure S4: Non-metric multidimensional scaling plot of juvenile fish densities showing assemblage differences between habitats (reef vs unstructured) and among locations.

Table S1: Biological data for all species detected as juveniles (in >3 deployments) in the restored shellfish reefs of Port Phillip Bay, Victoria, and Glenelg, South Australia.

Table S2: Performance metrics for the detection models used in assessing fish abundance.