High densities of large tuaki, the New Zealand cockle *Austrovenus stutchburyi*, provide a post-settlement predation refuge for conspecific juveniles

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ABSTRACT: Bivalves are ecosystem engineers, and their effective management relies on a full understanding of the mechanisms that influence population dynamics. Juvenile tuaki (New Zealand cockle) *Austrovenus stutchburyi*, a numerically dominant and ecologically important bivalve in New Zealand estuaries, were found at higher densities when surrounded by high densities of large adults within Waitati Inlet, in southern New Zealand. Consequently, we hypothesised that adults provided a refuge from predation for juveniles, resulting in higher juvenile survival and retention in dense beds. The observed pattern was consistent with post-settlement Allee effects, where declines in density and truncated size distributions may have resulted in unsuccessful recruitment if a density threshold was reached. Field experiments were undertaken in 2020 and 2021 to test the potential sheltering effect of adults on retention and survival of juveniles, with and without the addition of organic loading of sediments. Presence of adults had significant effects on juvenile retention and interaction with organic loading in 2020, but not in 2021. To isolate the effects of adult presence on predation of juveniles, a series of laboratory experiments were carried out using the predatory crab *Ovalipes catharus*. Juvenile survivorship from crab predation was enhanced in the presence of large adults, consistent with the hypothesised sheltering effect. Further, predation rates increased significantly from winter to summer, which correlated with increasing water temperatures and the breeding and moult cycle of crabs. These findings across surveys, field and laboratory manipulations have significant implications for effective fisheries management and restoration of bed-forming bivalves.

KEY WORDS: Adult—juvenile interactions · Bivalve · Predation · Cumulative stressors · Allee effect · Bivalve recruitment · Facilitation · Ecosystem engineer · *Austrovenus stutchburyi*

1. INTRODUCTION

Bivalves are a diverse taxonomic group that have commercial, cultural and ecological significance worldwide but have also been subject to multiple anthropogenic stressors at a global scale (Barber et al. 2015, Kreeger et al. 2018). For example, estuarine bivalve populations in Aotearoa New Zealand have been increasingly subject to environmental stressors arising from habitat conversion, coastal warming, eutrophication and overfishing (e.g. Tallis et al. 2004, Wells et al. 2019, Salmond & Wing 2022, 2023). Multiple stressors on estuarine bivalve populations may be additive or interact synergistically becoming cumulative, resulting in surprising and larger effects than individual stressors, and can precipitate dramatic ecosystem change (Crain et al. 2008, Crotty et al. 2017, Thrush et al. 2021, Salmond & Wing 2022, 2023).

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When stressors cause mortality events that reduce abundance or isolate a population, the surviving members may experience Allee effects, or declining per capita fitness with reductions in density. Allee effect density thresholds can occur when declines in density of individuals reach a tipping point below which there is reproductive failure, leading to further reductions in density and potential local extirpation (Allee 1931, Stephens et al. 1999, Gascoigne & Lipcius 2004, Aalto et al. 2019). In animals with complex life histories, or adult and larval phases, Allee effects can occur pre-settlement, for example on fertilisation success, and post-settlement, such as the effect of adult density on survival of recruits (Quinn et al. 1993, Wing et al. 1998). Post-settlement Allee effect thresholds can act on the survival of juvenile life stages, when vulnerability to a range of stressors, including predation, are typically at their highest. In some species, adult presence can increase the survival of conspecific juveniles by providing a refuge from predation through their morphology or behaviour (Tegner & Dayton 1977, Highsmith 1982, Childress & Herrnkind 2001). These effects may be particularly important for maintenance of recruitment into high-density bivalve beds.

In New Zealand, Allee effects may be an important component of the population dynamics of a venerid bivalve, the New Zealand cockle *Austrovenus stutchburyi* (hereafter referred to by its indigenous Māori name, 'tuaki'), an essential ecosystem engineer of local estuarine systems. Tuaki provide important services for the system by filtering water, providing substratum for other organisms, bioturbating sediments and acting as a vector for fluxes of nutrients and organic matter (Gibbs & Hewitt 2004, Savage et al. 2012, O'Connell-Milne et al. 2016, 2020, Thomas et al. 2021). Larval tuaki tend to settle out in areas of high adult aggregation due to environmental cues (Marsden & Adkins 2010). However, the importance of post-settlement processes of juvenile tuaki for population persistence are generally not well known (Marsden & Adkins 2010, Hunt et al. 2020).

Post-settlement adult—juvenile associations in estuarine species can be positive, neutral or negative (Thrush et al. 1996). Adult presence can benefit juvenile survival, for example through bioturbation that ameliorates oxygen-induced stress and increases food availability, but can also impinge on the survival of settled recruits by direct predation or competition for resources (Thomas et al. 2021). Uncertainty exists about the significance of adult—juvenile interactions in tuaki. For example, in northern New Zealand, Thrush et al. (1996) investigated interactions between adult and juvenile tuaki at sandy and muddy sites and found no pattern of association within study plots, concluding that juvenile distributions may have been influenced by larger-scale processes than adult presence. Further, Legendre et al. (1997) modelled the spatial distribution of tuaki within the same harbour and found no clear evidence for adult—juvenile interactions at a large scale. In contrast, in southern New Zealand where tuaki are found at much higher densities and with larger adult size distributions, no such conspecific interaction experiments on tuaki have been conducted.

Predation has been previously discussed as an important factor in southern tuaki population structure and could contribute to Allee effects by removing sheltering adults or inducing size-specific mortality on juveniles. For example, Thomas et al. (2021) concluded that avian predation may have been a significant limiting factor for juvenile tuaki biomass in southern New Zealand. Throughout both northern and southern New Zealand, tuaki are prey to a multitude of estuarine species including crabs, wading birds, whelks and coastal fishes, particularly large rays that enter estuaries on high tide (Legendre et al. 1997, Thrush 1999). Juvenile tuaki have weaker shells than large adults, leaving them vulnerable to predatory species such as wading birds (Rutten et al. 2006) and the commercially important portunid crab *Ovalipes catharus* (hereafter referred to by its common name, paddle crab) which can crush tuaki shells with its strong chelae (Davidson 1987, Jester et al. 2009). Anecdotal evidence has highlighted an increase in paddle crabs in New Zealand coastal waters, as well as a proliferation of invasive Asian paddle crabs *Charybdis japonica* in northern New Zealand, leading to rising concerns about their potential role in localised bivalve decline (Ministry for Primary Industries 2023).

A number of factors aside from natural predation threaten tuaki populations, in part by creating the potential for strong Allee effects. Tuaki are typically found in very high densities and rely on these high densities to reproduce through broadcast spawning (Stephenson 1981). However, evidence indicates large-scale declines of tuaki beds in many areas of New Zealand's estuaries due to anthropogenic stressors, particularly those arising from catchment modifications (Tallis et al. 2004, Rutger & Wing 2006, McLeod & Wing 2008, Wells et al. 2019). For example, nitrogen loading of estuaries has markedly increased in New Zealand as a result of agricultural intensification (Heggie & Savage 2009, Schlieman et al. 2022), causing a greater frequency of nuisance

blooms of the macroalgae *Ulva* spp. (Zeldis et al. 2011, Robertson & Savage 2021). Macroalgal blooms can induce sediment hypoxia in estuaries with consequent impacts on organism behaviour (Nelson et al. 2015, Paerl et al. 2018). Hypoxia associated with eutrophication has been demonstrated to affect tuaki behaviour, such as decreased individual burrowing depth, which can leave tuaki more vulnerable to predation (Marsden & Bressington 2009). In other areas of the world, large population crashes of bivalves have been observed as a result of eutrophic events (Peterson et al. 1994, Green-Gavrielidis et al. 2018). Bivalve population decline may result in a population reaching an Allee-effect threshold below which the population can experience reproductive failure (Levitan & McGovern 2005). Accordingly, Tricklebank et al. (2021) advocated for further research to understand mechanisms for Allee effects in tuaki populations to be a vital requirement in order to better inform management decisions.

The New Zealand tuaki fishery was established in 2002 under the Quota Management System, a framework of fisheries management based on hard-line yield-based biomass targets that do not typically incorporate aspects of species biology or local ecology (Durante et al. 2020). The New Zealand government has made mention of moving towards an 'ecosystem-based management framework' in several fisheries-related documents (Reid & Rout 2020). Although officially undefined, marine ecosystem-based management (EBM) is regarded as a multi-species approach to fisheries management that incorporates ecological principles and evidence-based recommendations, including protecting critical habitats and maintaining a species at a level where it can fulfil its ecological role in the ecosystem (Hewitt et al. 2022). In their review of EBM policy in New Zealand, Urlich et al. (2022) highlighted that effective EBM practices are likely place- and context-specific, and therefore there may be a need to reconcile the differences between centralised and local regulatory policy for the management of coastal resources.

The present study focuses on the understanding of tuaki population structure and the potential post-settlement Allee effects that may modulate predation rates on juvenile abundance. The first portion of the study utilises both field surveys to investigate adult—juvenile tuaki density and size structure, and manipulative field experiments based at Waitati Inlet. The field experiments were run over a 2 yr period to understand the potential sheltering effects of adult tuaki presence on the survivorship and persistence of juvenile conspecifics under both ambient and organi-

cally loaded conditions. We hypothesised that in the absence of adult conspecifics, juvenile tuaki would be found in reduced densities due to either migration or mortality from predation. The second portion of the study aimed to isolate the potential interaction of adult tuaki presence and predation by the paddle crab *Ovalipes catharus* on patterns of juvenile tuaki survivorship. We hypothesised that adult tuaki presence would increase juvenile survivorship, by providing a 'pavement' of high-density protection. The results from the present study fill a gap in understanding how adult tuaki presence and mature size distributions can influence juvenile tuaki persistence under intense predation pressure, with potentially significant application to management and restoration of bivalve populations.

2. MATERIALS AND METHODS

2.1. Study sites

Waitati Inlet (45° 43′ 19.64″ S, 170° 35′ 42.35″ E) is a large semi-enclosed estuarine system in the Otago region of southern New Zealand that receives inputs from the Waitati River and several smaller tributaries. Waitati Inlet was classed in 2015 as a shallow intertidal-dominated estuary with relatively low nitrogen loading, high tidal flushing and consequently relatively low symptoms of eutrophication (Robertson et al. 2016). Nevertheless, more recent observations of increasing land-based and urban sewage nitrogen inputs and associated blooms of *Ulva* spp. have caused community concern for the eutrophication status of the inlet (Langhans et al. 2022). Waitati Inlet is an area of particularly high tuaki density, with reports of average densities of up to 1800—3500 ind. m^{-2} (O'Connell Milne et al. 2020). The high densities of adults indicated that the area was an ideal location for the observations and field experiments in the present study. We observed abundant paddle crabs in the subtidal regions of the inlet, with incidence of observations higher at the estuary entrance and increasing in spring and summer months.

2.2. Observations

Four replicate transect lines were placed at 2 study sites (Fig. 1) on 2 dates in October 2022 during 0.25 and 0.3 m low tidal periods. Quadrats of 0.25 × 0.25 m were placed at 6 m intervals throughout the intermediate tidal zone, which, based on previous surveys,
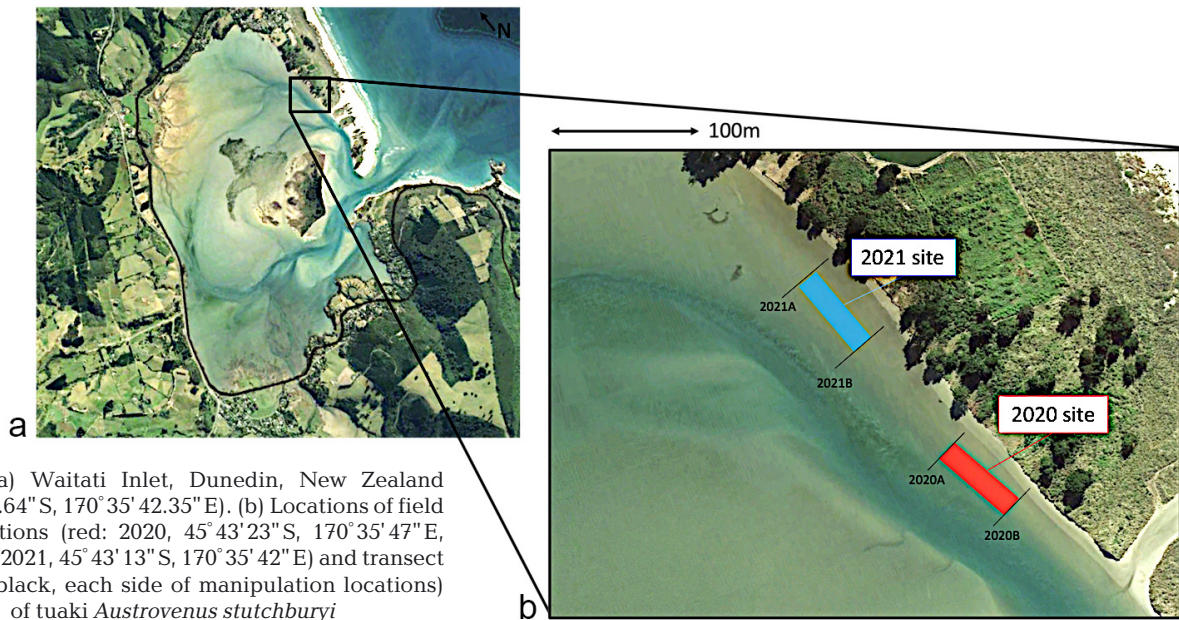
Fig. 1. (a) Waitati Inlet, Dunedin, New Zealand (45° 43' 19.64" S, 170° 35' 42.35" E). (b) Locations of field manipulations (red: 2020, 45° 43' 23" S, 170° 35' 47" E, and blue: 2021, 45° 43' 13" S, 170° 35' 42" E) and transect surveys (black, each side of manipulation locations) of tuaki *Austrovenus stutchburyi*

was the area of highest tuaki density. Sediment was excavated from the quadrat to 5 cm depth and rinsed through a 5 mm sieve. All tuaki were removed and measured along their longest axis to the nearest millimetre using Vernier callipers. To get an indication of relative shell area coverage based on size of an individual tuaki, we calculated the projected surface area of a subsample of tuaki between a size range of 5 and 50 mm (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m726p085_supp.pdf). These values were then plotted and the line of best fit was determined (Fig. S1). The relationship was then used to predict the surface area of the ventral side of the tuaki based on its length, providing a conversion of tuaki size distributions to estimate shell surface area per square metre. The resulting metric provided a variable that incorporated both the size distribution and the density of adult tuaki comprising a bed.

2.3. Field manipulation

Replicated field experiments were carried out in December 2020 and December 2021 to resolve the effects of adults on the retention of juvenile tuaki among treatments. For the experiment, we set up 5 blocks (6 × 4 m area), consisting of 4 randomly placed treatments within each block. The block sites for 2020 and 2021 were 100 m apart and had almost identical tidal immersion periods. We assigned fully crossed combinations of 2 factors to each treatment within the blocks: presence/absence of adult tuaki and enhanced concentrations of *Ulva* spp. detritus in the sediments.

In all treatments, 50 pre-tagged juveniles between 6 and 15 mm (with the same size ratios across all treatments) were added to the centre of a 0.25 m² plot, and monitored for 1 h to ensure they buried and avoided immediate predation. The 0.25 m² plot size was chosen as it was used in a successful tuaki transplant experiment by Stewart & Creese (2002). Additionally, in the 2021 experiment, we tagged juveniles in the experimental plots with non-toxic nail polish to determine how many migrated in or out of the plot.

All experimental areas were cleared of any tuaki and sediment to 10 cm depth. Sediment was then returned and adult tuaki were added at the density required for each of the 4 treatments. To test for the effects of adult presence on juvenile survivorship, 250 adult tuaki were added to 2 treatment plots within each block. The treatment density (1000 adults m⁻²) was reflective of those previously surveyed within Waitati Inlet (Wing et al. 2002). Adult tuaki that were added back into treatments were collected by finger ploughing from within several metres of the quadrat and kept in buckets for less than 1 h before addition to each plot. We observed no mortality of adults induced by handling stress, and no indication of adult mortality on resampling of the experiment. Adult tuaki were defined as any healthy individual measuring a minimum of 25 mm across its longest axis, a size assumed to be generally beyond predation risk (Cummings et al. 2007).

To simulate the effect of decomposition of macroalgal bloom detritus, 50 g (200 g dry wt m⁻²) of dried, homogenized non-enteromorphic *Ulva* was mixed into a 500 ml slurry with sediment and water, then

incorporated into the surface layer of all organically enhanced treatment plots following the addition of any adult tuaki. We expected that over the experimental period of 14 d, the breakdown of the *Ulva* detritus would stimulate microbial processes that consume oxygen and replicate the hypoxic effects of a eutrophic event in these intertidal estuaries. A range of methods have been used in past manipulations to replicate organic loading in estuarine environments, including dried and pulverised *Ulva* in mesocosms (Karlson et al. 2016, 2021), fresh *Ulva* both bagged in the field and unbagged in experimental tanks (Marsden & Bressington 2009) and cornflour in experimental field plots when *Ulva* could not be sourced (Lohrer et al. 2012). For the present manipulation, high volumes of dried and ground *Ulva* were used to minimise the effects of *Ulva* age, size or other biotic factors on sediment conditions and to ensure that degradation would have a short-term effect on sediment conditions. To simulate the effect of disturbing surface sediments, we similarly massaged the top layer of all non-organically enhanced treatments after addition of juveniles. Finally, a 0.5 m 'buffer zone' was cleared using the same methods around each replicate to easily track any tagged juvenile migration into the buffer zone.

After 2 wk, the experimental plots were excavated to 10 cm depth. Juvenile tuaki were retrieved from treatments through finger ploughing of plots in 2020 and sediment was sieved to 5 mm in 2021 to ensure all tuaki were collected. In both years, all living tuaki excavated from the sediments were collected, counted and measured. The surrounding buffer zone of 0.5 m was also excavated and any tagged juveniles were recorded and measured.

A generalised linear mixed effects model was run with adult tuaki presence, *Ulva* addition and *Ulva* × presence as predictors and treatment block as a random factor (JMP Pro ver. 15.2.0). A post hoc Student's *t*-test was then run to determine the significant differences among groups based on $p \leq 0.05$. The 2020 and 2021 datasets were analysed individually, then combined, with the *Ulva* factor removed and the year of each study added as a predictor.

2.4. Laboratory predation trials

Laboratory trials were run to isolate the effect of paddle crab predation on survival of juvenile tuaki in the presence and absence of high densities of adults. Paddle crabs were collected from Otago Harbour in <10 m depth. Retained individuals were between 68 and 115 mm in carapace width and had all limbs intact, and both female and male crabs were used in the trials. Individual crabs were pulled randomly from a pool of >40 available individuals and were used in trials up to 3 times.

Sediment for the tanks was collected from surface sediments at the Warrington domain section of Waitati Inlet at low tide. All sediments were rinsed through 1 mm sieves to ensure no large living organisms or shell hash entered the tanks. Sediment was then hand-mixed to a homogeneous quality and added into each tank to 5 cm depth. Each tank of 27 × 46 × 58 cm dimensions in the experimental array was supplied with flow-through seawater collected locally at ambient environmental conditions (~70 l). Water flow for all tanks was kept constant (approximately 3.5 l min^{-1}, or 3 total turnovers per hour), and a weighted air-stone was provided to ensure that water stayed well oxygenated and circulated.

Six predation experimental trials were run across 2 time periods: a winter period (May−July 2022) and a summer period (December 2022−March 2023). Sea surface temperature of the Otago Harbour (the source of flow-through water for treatment tanks) ranged from 7 to 12°C in the winter period, and from 16 to 21°C in the summer period. All adult tuaki used in the manipulations were between 38 and 55 mm along their longest axis. To ensure that cumulative adult area would not have a confounding effect on the study, adults were divided into 2 size classes: 38−45 and >45 mm. An even ratio of these size classes was used for each replicate in the adult density treatments. Two adult density treatments were used (400 and 800 m^{-2}), reflective of the densities recorded in our field survey. These treatments were later combined in our analysis to a single 'high density' treatment due to the observed similarity of their effects on juvenile survival.

Treatments were divided into those with a density of adults ≥ 400 ind. m^{-2} and treatments with no adult tuaki present. We collected all tuaki from Waitati inlet toward the mean low tide level, where they would have been very likely to encounter paddle crabs prior to collection. Fifty juveniles between 6 and 15 mm were then added to each tank along with adults and spread across the sediment evenly. Tanks were then left to settle for at least 12 h, allowing tuaki to burrow into the sediment. An even range of juvenile tuaki sizes was used across the treatments to ensure juvenile size had no effect on crab predation rate (see Table S2).

After the acclimation period, 1 adult paddle crab was added to each tank and left for a 48 h feeding trial. We randomly selected and assigned crabs to treat-

ment tanks. Crabs were starved for 48 h prior to addition to the feeding trials, reflective of environmental periods of non-feeding (Haddon et al. 1987). Once the 48 h feeding trial was complete, crabs were removed from their respective treatment tanks, measured for size along the longest axis of their carapace, and sex was determined. We then measured and counted all remaining juvenile tuaki from each treatment. Between each round of experiments, sediments were remixed and redistributed between tanks, and the treatments within each tank were randomly reassigned.

To determine the relationships and interactions between treatments, season and predation rates by paddle crabs, a generalised linear additive model for location, scale and shape (GAMLSS) was run in R (version 4.0.3) (Stasinopoulos et al. 2017). Specifically, we included adult tuaki presence, season and crab sex as predictors and size of predating crab as a cofactor. To simplify model outputs, the seasons of the trial were split into a binary of 'cool' trials (those undertaken in May, June and July 2022) and 'warm' trials (those undertaken in December 2022, January and March 2023). Sea surface temperature data at Portobello Marine laboratory was collected hourly via a telemetered AquaTROLL 500 Multiparameter Sonde during the period of trials.

3. RESULTS

3.1. Observations

The observations of juvenile and adult tuaki abundance in Waitati Inlet revealed that the density of juvenile tuaki (m^{-2}) increased exponentially with density of adults (m^{-2}) ($y = 19.287 \times e^{0.0019139x}$, $r^2 = 0.217$) (Fig. 2a). When the x-axis was converted into the projected surface area, much of the variation in the higher densities was explained, and the exponential model explained an additional 46% of the variance ($y = 18.19 \times e^{2.649x}$, $r^2 = 0.674$) (Fig. 2b).

When represented on a 3D surface plot, our survey demonstrated that as density and median size of a tuaki sample increased, so did the percentage of surface area projected to be covered by adult tuaki (Fig. 3). The negative slope of isoclines indicated that as the median size of a tuaki population increased, it took a lower density of tuaki to achieve a higher projected surface area covered. The projected surface area exceeds 1 m^2 in some replicates because it is a 3-dimensional measurement (tuaki will commonly bury down to 5 cm depth, or face valve up) projected onto a 2D plane.
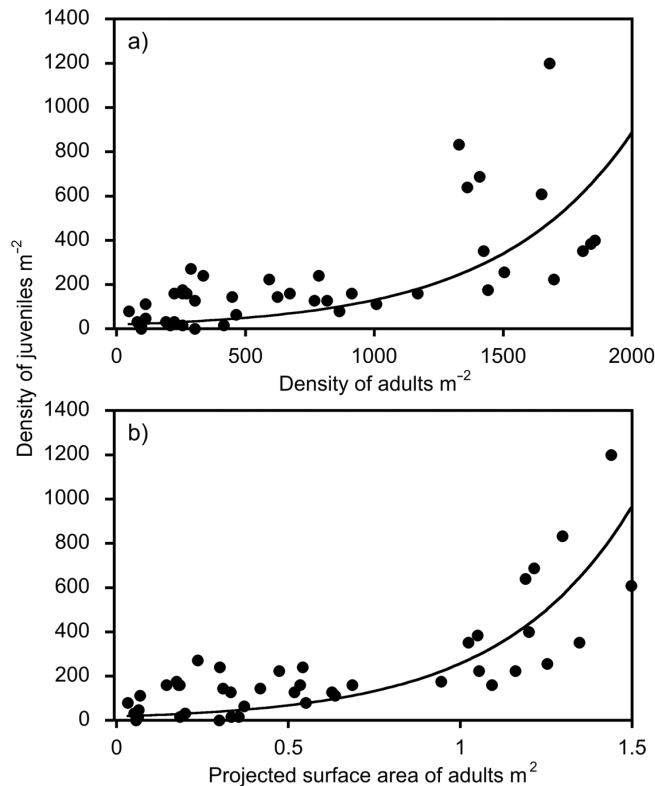

Fig. 2. (a) Modelled relationship between the density of adult tuaki *Austrovenus stutchburyi* (m^{-2}) and the density of juvenile tuaki (m^{-2}) at Waitati Inlet, Dunedin, New Zealand, during an October 2022 transect and quadrat survey ($r^2 = 0.217$, N = 36). (b) Modelled relationship between the projected surface area covered by adult tuaki (m^2) and the density of juvenile tuaki (m^{-2}) during an October 2022 transect and quadrat survey ($r^2 = 0.674$, N = 36)

3.2. Field manipulations

The generalised linear model for the 2020 manipulation revealed a significant interaction between the effects of adult tuaki presence and organic loading on juvenile tuaki retention ($F_{7,19} = 5.3157$, p = 0.0058). The fixed effect test revealed that adult tuaki presence had a statistically significant positive effect on juvenile tuaki retention ($F_{1,19}$, p = 0.0206), but *Ulva* presence had no significant effect at 95% confidence ($F_{7,19} = 4.2286$, p = 0.0622). The average proportion of juveniles remaining was highest in the 2 adult treatments, followed by the juveniles only with no added *Ulva* treatment, and lastly the juveniles only and *Ulva* treatment. The Student's *t* post hoc analysis revealed that the treatment with adult absence and *Ulva* addition was significantly different from the adult addition treatments, while the absence of adults without the addition of *Ulva* did not yield significantly lower retention of juveniles (Fig. 4a).
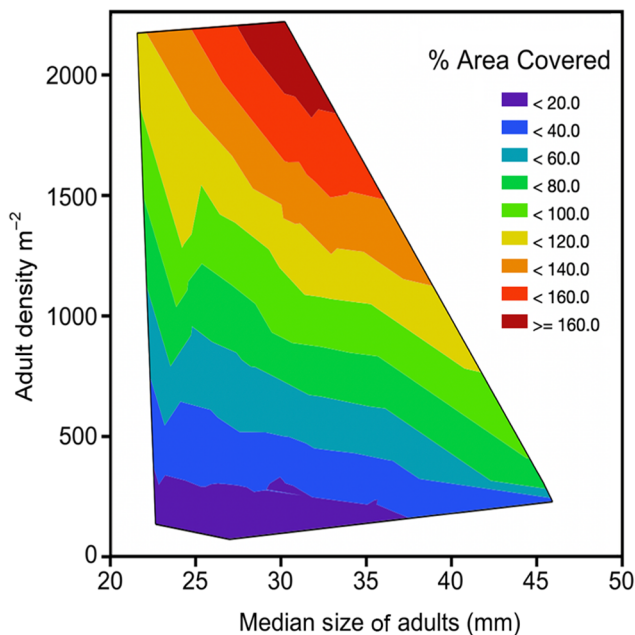
3.3. Laboratory manipulations

Proportions of juveniles consumed across all trials and treatments ranged from 0 to 1. The outputs of the GAMLSS model revealed that season, crab sex and the presence of adult tuaki all had a significant effect on the proportion of juvenile tuaki consumed in the study (Table 2). The effect of crab size on proportion of juvenile tuaki consumed was not statistically significant, comprising a weak effect compared to those of season, sex and adult presence (Table 2). The odds of juveniles being consumed were approximately 5 times higher for female crab treatments compared with male crab treatments (Fig. 5, Table 3).

When averaged across seasons, the estimated proportion eaten with no adults present was 0.50 (95% CI: 0.38, 0.62) compared with 0.12 (95% CI: 0.08, 0.17) when adults were present, which equates to an odds ratio of 7.29 (Table 3). Although the interaction effect between season and adult presence was not statistically significant (p =

Fig. 3. Surface plot comparing median size of sampled adult tuaki *Austrovenus stutchburyi* in mm, with the density (m^{-2}) of sampled adult tuaki. Colours of plot represent the percentage of the projected surface area (m^2) covered by adult tuaki as a function of their density and size. Data were obtained from transect surveys undertaken in Waitati Inlet, Dunedin, New Zealand, in October 2022. N = 60

Conversely, the generalised linear model for the 2021 manipulation revealed no statistically significant relationships between the effects of adult tuaki presence and organic loading on juvenile tuaki retention ($F_{7,19}$ = 0.8592, p = 0.5628), and none of the average proportions was significantly different among treatments (Fig. 4b). Proportions of excavated: outplanted juveniles exceeded 1 in most replicates in 2021, meaning we extracted more juveniles than we originally put into experimental plots. Significantly more tagged juveniles were retrieved from treatments than untagged juveniles ($F_{1,19}$ = 18.385, p < 0.001). In all cases except one, 3 or fewer tagged juveniles were retrieved from the 0.5 m buffer zone (Table 1).

Because the effect of organic loading via *Ulva* addition was not consistent and unidirectional across years, we removed *Ulva* as a factor from subsequent model runs to focus on the effects of adult presence on juvenile retention. The fixed-effect test of the generalised linear model comparing year groups and adult density revealed a significant effect of study year on juvenile tuaki retention ($F_{1,8}$, p = 0.0015), and of the interaction of year and adult density of the treatment ($F_{1,28}$, p = 0.0166).
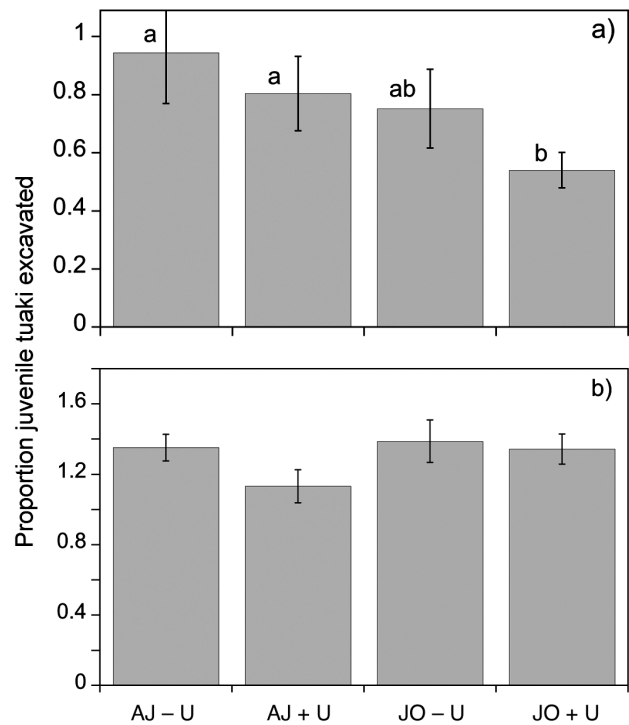

Fig. 4. Proportions of juvenile tuaki *Austrovenus stutchburyi* excavated from the 4 treatments of the field manipulation in (a) December 2020 and (b) December 2021. AJ − U: adult tuaki presence and no *Ulva* added; AJ + U: adult tuaki presence and *Ulva* added; JO − U: juveniles only and no *Ulva* added; and JO + U: juveniles only with *Ulva* added. N = 20. Letters denote levels of significance as determined by Student's *t* post hoc test at α = 0.05. Error bars are SE

Table 1. Experimental block, treatment type (AJ − U: adult tuaki presence and no *Ulva* added; AJ + U: adult tuaki presence and *Ulva* added; JO − U: juvenile tuaki only and no *Ulva* added; and JO + U: juvenile tuaki only with *Ulva* added), number of tagged juveniles found within the 0.25 m^2 experimental plot, number of tagged juveniles found within the 0.5 m surrounding buffer zone and the number of untagged juveniles found within the 0.25 m^2 experimental plot in the 2021 field manipulation at Waitati Inlet, Dunedin, New Zealand

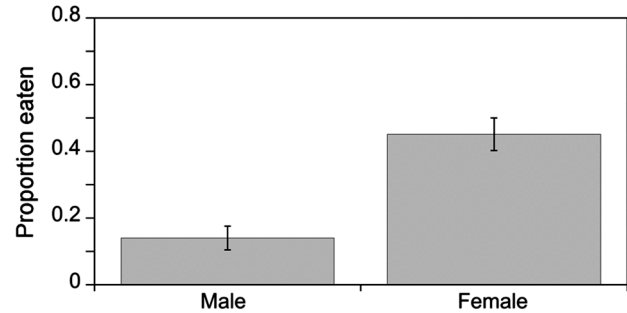| Block	Treatment	Tagged juveniles in plot	Tagged juveniles in buffer zone	Untagged juveniles in plot
1	AJ − U	33	0	37
	AJ + U	25	1	14
	JO − U	45	2	22
	JO + U	39	2	24
2	AJ − U	39	5	30
	AJ + U	39	0	21
	JO − U	39	0	31
	JO + U	42	3	40
3	AJ − U	33	1	21
	AJ + U	33	0	27
	JO − U	37	0	43
	JO + U	39	3	30
4	AJ − U	42	1	35
	AJ + U	43	0	24
	JO − U	35	0	13
	JO + U	40	1	16
5	AJ − U	42	1	26
	AJ + U	33	3	24
	JO − U	37	2	45
	JO + U	35	0	31

Fig. 5. Average proportions of juvenile tuaki *Austrovenus stutchburyi* consumed by paddle crabs *Ovalipes catharus* in treatments averaged across the effect of crab sex. Error bars represent 95% confidence intervals

lower than the odds of predation in warm conditions (Table 3). The average proportions of juvenile cockles consumed by paddle crabs in the treatments with no adults were higher relative to those treatments with adults present in trials during the summer (January to March) warm period (15−20°C) when compared with consumption during the colder (<10°C) winter period (June to July) (Fig. 7).

4. DISCUSSION

The results of our study are consistent with a large effect of adult tuaki presence on juvenile retention and survival within mature, high-density beds. Our observational survey data indicated an exponential, positive association between adult tuaki and juveniles within their naturally occurring distributions in mid-intertidal beds. The contrasting results from the field manipulations between the 2 years indicate context-specific effects of presence of high-density adult beds and organic loading on juvenile retention. By specifically controlling for predation pressure in a laboratory experiment, we demonstrated that presence of adult tuaki at high densities provided a refuge

0.058) the model suggests there is a tendency for the effect of adult presence to be stronger in the warm season. This is shown in Fig. 6 and Table 3, where the adult present/not-present odds ratio is higher (13.53) in warm conditions than in cooler conditions (3.93). Predation was higher during warm seasons (Fig. 6), particularly when no adults were present, where the odds of predation in cool conditions were 0.070 times

Table 2. Estimated generalised linear additive model for location, scale and shape (GAMLSS) model parameters for the mean effect of crab size, sex, trial season and presence of adult tuaki *Austrovenus stutchburyi* on predation rates of juvenile tuaki by paddle crabs *Ovalipes catharus*. Parameters are presented on the logit scale. Asterisks represent predictors with statistical significance below the 0.05 significance level

Model parameter	Estimate	SE	t	p
Intercept	2.40564	1.54718	1.555	0.125
Crab size	−0.03338	0.01710	−1.952	0.0549
Season (Warm)	2.65905	0.48564	5.475	<0.001*
Crab sex (Male)	−1.62004	0.36078	−4.490	<0.001*
Adult presence (Present)	−1.36821	0.47417	−2.886	0.00519*
Season: Adult Presence (Warm:Present)	−1.23687	0.64062	−1.931	0.0576

Table 3. Pairwise comparisons of the odds ratio (OR) of predation likelihood by paddle crabs *Ovalipes catharus* on juvenile tuaki *Austrovenus stutchburyi* when adult tuaki are present or absent, when the predator is female or male, in the cool (May, June and July 2022) or warm seasons (December 2022, January and February 2023) and in the presence or absence of large adult conspecifics. Standard error (SE), lower confidence limit (LCL) and upper confidence limit (UCL) are provided for each OR estimate. Each of the tests resulted in significant effects as indicated by p values below 0.05

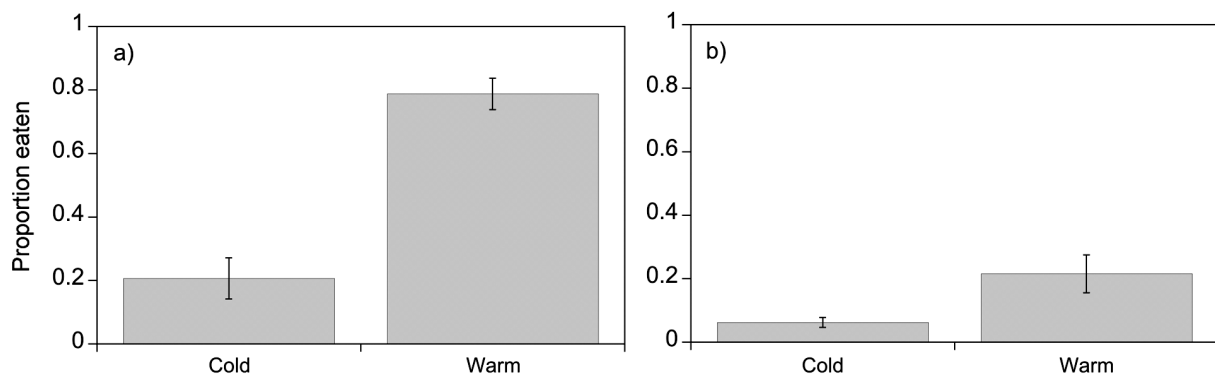| Contrast	OR	SE	LCL	UCL	z-ratio	p
No adults/Adults present	7.29	2.36	3.87	13.7	6.146	<0.001
Female/Male	5.05	1.82	2.49	10.2	4.490	<0.001
Cool/Warm (no adults)	0.070	0.034	0.027	0.181	−5.475	<0.001
Cool/Warm (adults present)	0.241	0.105	0.103	0.564	−3.282	0.001
No adults/Adults present (cool)	3.93	1.86	1.55	9.95	2.886	0.0039
No adults/Adults present (warm)	13.53	5.89	5.77	31.75	5.897	<0.001

Fig. 6. Average proportions of juvenile tuaki *Austrovenus stutchburyi* consumed by paddle crabs *Ovalipes catharus* in the (a) absence and (b) presence of high-density adult conspecifics, during the cooler periods of May, June and July 2022 ('cold') and the warmer periods of December 2022, January and February 2023 ('warm'). Error bars represent 95% confidence intervals

for juvenile tuaki from predation by paddle crabs.

Our survey results provide convincing evidence that high densities of larger tuaki were strongly associated with the high density of juveniles. It would be expected that if adult density had no effect on juvenile presence, then juvenile tuaki density would be independent of adult density. Instead, we found that in areas of low adult tuaki density, independent of tidal height, juvenile tuaki may have either preferentially or passively migrated toward areas of high adult density where they were retained, or were lost to predation during migration or due to lack of shelter from adults. Similarly, Stewart & Creese (2002) found high mortality rates of smaller size classes of tuaki (10−18 mm) when transplanted into experimental plots with no larger tuaki present, a pattern they attributed to predation.
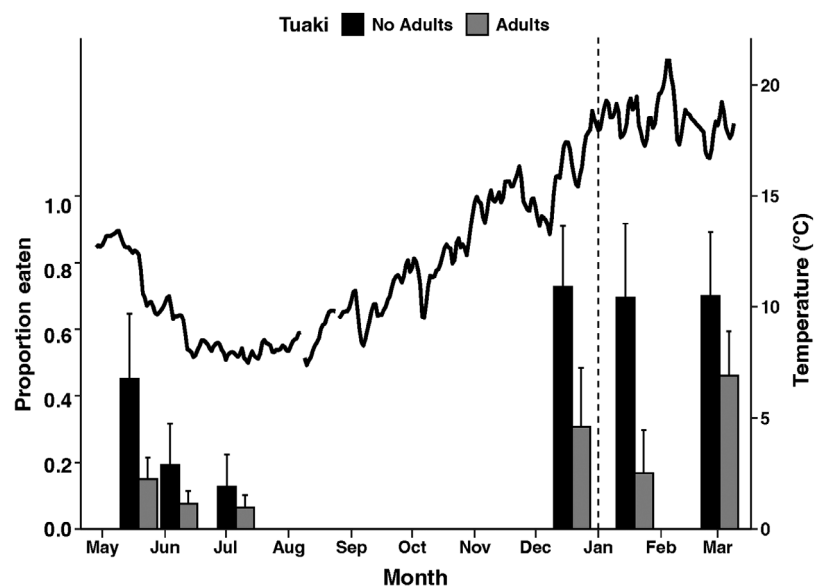

Fig. 7. Proportion of juvenile tuaki *Austrovenus stutchburyi* consumed by paddle crabs *Ovalipes catharus* in treatments with adult tuaki (grey bars) and without adults (black bars) among trials over the months of study overlaid onto a line graph of sea surface temperature data from Otago Harbour. Dashed line indicates beginning of year. Bars represent standard error within each trial

Projected tuaki surface area explained significantly more of the variation in juvenile densities than did adult density, suggesting that the coverage effect of larger adults, and the associated protection from predation, may have contributed to juvenile density more strongly than adult numbers alone. In our survey, mature size distributions and high density of tuaki produced projected coverages of adult tuaki m^{-2} that were over 100% of the area covered. It is likely that the presence of adult tuaki provided other benefits to juvenile tuaki retention and survival, such as increased access to nutrition through their mixing of the benthic boundary layer (Thomas et al. 2021). The physical presence of large adults may also reduce the rate of juvenile emigration by providing stabilisation of the surrounding sediment and reducing the likelihood of juvenile dispersal via bedload transport (Lundquist et al. 2004). The field and laboratory manipulations were then undertaken to test the importance of the hypothesised sheltering effect of adults for juvenile retention and survival.

In the 2020 field manipulation, juvenile tuaki retention was significantly higher in treatments with adult tuaki, and lowest in the crossed treatment with organic loading. In 2021, there were no effects resolved of adult presence or organic loading on juvenile retention within treatments, although power was relatively low in both trials. Despite concerns of increased nuisance *Ulva* blooms in Waitati Inlet (Langhans et al. 2022) and their marked effect on tuaki behaviour through effects on sediments (e.g. Marsden & Adkins 2010), the effect of experimental organic loading was small when not crossed with adult absence in 2020, and had no apparent effects in 2021. The lack of effect may have been due to the small-scale treatments not accurately reflecting the scale of a system-wide macroalgal bloom and concomitant changes in sediment biogeochemistry. The presence of tagged juveniles in the excavated buffer zones and untagged juveniles within the experimental plots at the conclusion of the experiment in 2021 indicated that juvenile redistribution occurred during the experiment. Hunt et al. (2020) highlighted the importance of small-scale dispersal of tuaki post-settlement for regulating community dynamics, as originally emphasised by Pilditch et al. (2015). Redistribution of juveniles through active migration and bedload transport may provide a buffer against areas becoming depleted of juvenile tuaki as a consequence of predation.

Our survey results demonstrated that juvenile tuaki tend to aggregate within areas of mature, high-density adult beds. The retainment of juveniles in the

2020 manipulation provided some evidence for a mechanism behind the observation, but the pattern was not replicated in the 2021 manipulation. The results of the 2021 field experiment may have been influenced by high density and turnover of juveniles saturating any predation effects; however, recruitment rates were not quantified in either year. It is also important to note here that predation pressure was not quantified or controlled for in either of the field experiments. Although the locations for each manipulation were less than 100 m apart, fine-scale gradients that affect tuaki distribution and abundance can exist within highly variable estuarine intertidal zones both across space and time (Larcombe 1971, Thrush et al. 2000, Ellis et al. 2002, McMullin et al. 2021). Even small spatial differences could result in different hydrodynamic pressures acting on juveniles (e.g. Thrush et al. 2000), meaning adult tuaki presence becomes more important for sediment stabilisation and consequent retention of juveniles in these areas. On a temporal scale, it is possible that post-settlement dynamics of tuaki may be determined by juvenile redistribution in some years, while in others predation may dominate.

The gap in knowledge surrounding the abundance and intensity of predation on our field manipulations provided the motivation for our laboratory trials, in order to isolate the potential effects of predation on juvenile tuaki in the absence of conspecific adult protection. The observed high predation rates in the juvenile-only treatments in the laboratory predation trials were consistent with the hypothesis that post-settlement Allee effects occur in tuaki populations. During the experiment, we observed paddle crabs picking up adult tuaki and setting them aside to either self-bury or access juvenile tuaki. Although not quantified, the increased handling time of adult tuaki provides a plausible mechanism by which adults could provide a refuge from predation for juvenile tuaki.

The time of year of the laboratory study also had a significant effect on predation rates. It is likely that the observed increase in juvenile mortality during the warmer trials was due to the physiological effects of higher temperatures on predator metabolism and foraging rates (Dell et al. 2014, Matassa & Trussell 2015, Csik et al. 2023). The high rates of predation observed for female paddle crabs in the warm trials are also consistent with the higher energetic needs before the females moult in early winter pre-copulation (Osborne 1987). Hostile pre-mating guarding behaviour by male paddle crabs as recorded by Haddon (1994) may result in a reduction in predation rates by both males and females during winter.

The interaction of adult presence and temperature shows that the sheltering effect of adult tuaki was greater during the warmer trials. When predation rates were high overall, juvenile mortality was significantly higher in the absence of adult protection; therefore, the presence of adults becomes more important for juvenile tuaki survival in the summer months. In situations where an adult tuaki population has faced mass mortality (i.e. following an acute environmental disturbance or intense, size-selective harvest), our results imply that strong post-settlement Allee effects may occur for newly settled recruits. In these circumstances, juveniles face the coupled challenge of temperature-induced increased predation rates and a lack of conspecific protection. The interaction of temperature and predation on juvenile survival observed in our laboratory experiment, coupled with our field experiment and survey data, imply that restoration efforts of tuaki beds would potentially be more effective in cooler periods and with high densities of adult tuaki, which would provide both bed structure and a shelter from predation for new recruits. If it is not possible to undertake restoration in the cooler seasons, the consideration of both density and average size of restored beds becomes more important to create appropriate sheltering surface area that effectively enhances post-settlement juvenile tuaki survival.

The observed interactions of temperature, predation and adult—juvenile tuaki associations could also have significant implications for the management of tuaki fisheries. Since 1986, tuaki have been commercially harvested from Waitati Inlet for domestic and international export (Irwin 2004). There has been no provision in the catch limits for catch spreading among the inlets in the region, highlighting the vulnerability of bivalve beds in individual inlets to overharvest. From 2010 to 2020, Waitati Inlet provided an average of half the total allowable commercial catch for the Otago region tuaki fishery, and from 2016 to 2018, it provided almost the entirety of the regional catch (Ministry for Primary Industries 2021), raising some concerns for sustainability and maintenance of mature size distributions. Our study demonstrates that significantly reducing adult tuaki densities can affect the retention and survival of juvenile recruits. These effects may increase in the future, with warming waters potentially allowing for the range expansion of more voracious bivalve predators such as the invasive paddle crab *Charybdis japonica* into southern waters (Fowler et al. 2013, Hilliam & Tuck 2023). The continued impact of eutrophic *Ulva* blooms, particularly as they occur most frequently during warm summer events (Paerl et al.

2018), could act as an additional stressor to new juveniles under temperature-enhanced consumption rates by resident predators. These issues highlight the importance of context-specific, local-level and adaptive management of shellfish beds.

Our study demonstrates the importance of the presence of high densities of adults for successful survival and recruitment in tuaki populations. Truncation of size distributions towards lower size classes can occur as a result of the selective harvest of larger size classes, as well as by other anthropogenic stressors such as organic loading (Hartill et al. 2005, Marsden & Adkins 2010, Wells et al. 2019). For example, Stewart (2005) found that in a highly eutrophic site in Tamaki, Auckland, adult tuaki sizes were small, not exceeding 25 mm. The loss of large individuals could impact the retention and survival of juvenile recruits into populations, by exponentially reducing the shelter provided by adult shell surface area. Our results highlight the inherent risks of using the current management targets based on biomass at 'maximum sustainable yield' (MSY) (Wing et al. 2002), which do not incorporate spatially discrete subpopulation dynamics or size structure. Similarly, MSY-based management principles do not account for Allee effects, the observed positive relationship between recruitment and adult density that we have demonstrated. Although tuaki are an endemic species to New Zealand, our findings are likely relevant to the management of bivalve beds globally. Recognition of the importance of Allee effects for effective management of bivalves can help inform communities of the potential risks of overharvest and the requirements of maintaining mature size distributions and high-density areas to support juvenile retention and recruitment into shellfish beds.

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