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Original research article Assessment of spatial fishing closures on beach clams

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ABSTRACT

Spatial fishing closures are typically implemented for conservation and fisheries benefits, but the effects of such initiatives are often not tested. This study examined whether the densities and size compositions of beach clams differed between commercially fished and non-fished zones on beaches. Sampling of clams was stratified across two habitats (swash and dry sand) on two commercially fished beaches, before and during (early and late) the 6-month harvesting period. Two beaches that had no commercial fishing were also sampled the same way and acted as external controls. Differences in densities, but not size compositions, of clams were evident between zones on the commercially fished and control beaches, but they were mostly apparent only across short (day and week) periods before, early and late harvesting, and thus were most likely pulse responses of clams to stochastic, non-fishing related events that acted independently across the different zones on each beach. The potential movements of clams along and across beaches as well as current restrictions on commercial fishing probably dampened detection of longer-term fishingrelated impacts and demographic differences in clams between commercially fished and non-fished zones. Direct fishing-related impacts on clams may only be discernable in the immediate vicinity of, and persist for a short period following, an actual fishing event on a beach. Nevertheless, the zones closed to commercial fishing may provide valuable protection to a portion of clams on each beach and alleviate beach-wide harvesting impacts. The broader value of these closed fishing zones requires knowledge of the impacts of fishing on other beach organisms and ecosystem functioning. Further experimentation that tests other aspects of management arrangements of beach clams may help determine their global applicability for sustainable harvesting, and contribute to the overall conservation management of sandy beach ecosystems.

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1. Introduction

Spatial closures to fishing are increasingly being incorporated into conservation and fisheries management strategies as a means to provide protection to wild populations of aquatic organisms from human exploitation (Lubchenco et al., 2003; Botsford et al., 2009; Lester et al., 2009). The most notable examples of such measures are no-take marine protected areas and reserves, which compared to openly fished areas have in many instances been shown to enhance the densities and sizes of organisms as well as aquatic biodiversity (Lester et al., 2009; Sciberras et al., 2013). Much of this evidence has been based on work done on fishes and invertebrates inhabiting shallow coastal rocky reefs (Barrett et al., 2007; Di Franco et al., 2009; Edgar and Barrett, 2012; Guidetti et al., 2014). Few studies have examined the effects of such management initiatives on the fauna inhabiting beaches.

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Sandy beaches are the most common type of shoreline bordering the world's oceans and among the most dynamic, but threatened, habitats worldwide (McLachlan and Brown, 2006; Schlacher et al., 2008; Defeo et al., 2009). Ocean beaches are culturally valuable and of high socio-economic importance as they provide extensive ecosystem services to humans (Schlacher et al., 2008; Defeo et al., 2009). Even so, many such beaches support diverse assemblages of benthic invertebrates and other fauna (McLachlan and Brown, 2006; Defeo and McLachlan, 2013). Beach clams (burrowing bivalve molluscs) often dominate the macrofaunal biomass of shallow subtidal and intertidal zones and contribute greatly to the ecology of high-energy ocean beach ecosystems in tropical and temperate regions (McLachlan et al., 1996; Defeo, 2003), but like many exploited benthic invertebrates (Anderson et al., 2011) population declines have been observed in several species (McLachlan et al., 1996; Defeo, 2003; Ortega et al., 2012). Various management initiatives to conserve beach clam populations have been implemented, including closed areas and times to harvesting, and quotas (Castilla and Defeo, 2001; Defeo, 2003). Rarely, however, has the success of such strategies been evaluated in an experimental manner (Walters and Holling, 1990; Underwood, 1995), thus limiting their global applicability for sustainable resource management.

The beach clam *Donax deltoides* supports significant fisheries throughout eastern and southern Australia, but in recent years there have been notable declines in population levels across its distribution, the causes of which have not been fully identified (Ferguson and Ward, 2014; Gray et al., 2014). In response to these declines and to appease social conflicts between commercial harvesters and other beach user groups, some east Australian beaches were zoned into fished and non-fished sections to commercial beach clam harvesting in 2010. Further to this, a six-month temporal closure to commercial harvesting was implemented across beaches in 2012 along with the introduction of a minimum shell length (SL) of 45 mm and a 40 kg per-day trip limit. Across all beaches, recreational and indigenous fishers are permitted to catch clams year round, but since 2010 they have not been permitted to remove clams from beaches due to toxin concerns and they can only be retained and used in-situ as bait. The presumed current total harvest from these two sectors is therefore considered low and may be <5% the total annual commercial harvest (Murray-Jones and Steffe, 2000). The harvesting of clams by all sectors is restricted to digging by hand. The impacts of these management arrangements on beach clams and in particular the potential value of the spatial closures to commercial fishing have not been assessed, and are the subject of investigation here.

The overall goal of this study was to evaluate the potential effects of within-beach spatial closures to commercial harvesting on beach clams. This was done by quantitatively sampling clams across two habitats in the commercially fished and non-fished zones on two beaches, before, early and late harvesting. This was done to specifically test the hypothesis that changes in the densities and size compositions of clams from before to during harvesting would differ between the commercially fished and non-fished zones on beaches. Because the potential impacts of commercial harvesting of clams may not be limited to just the fished zones on beaches but also the non-fished zones, two delineated zones across two non-commercially fished beaches were also sampled in the same way and acted as external controls, thus providing a before versus after, control versus impact (BACI) type assessment. The results are discussed in terms of management strategy evaluation and sandy beach ecology and conservation.

2. Methods

2.1. Experimental design and sampling

The two commercially fished study beaches were South Ballina (-28.95, 153.51; 30 km long) and Stockton (-32.80, 151.88; 32 km), with the northern 5 and 3 km of each beach, respectively, being closed to commercial fishing. The sampling of the commercially fished zone on each beach was limited to a 6 km section where commercial fishing effort is most concentrated, and immediately abutted the non-fished zone. A total of 6 commercial fishers reported harvesting clams on each beach throughout the study period. The two non-commercially fished control beaches were Sandon (-29.64, 153.32; 7.3 km) and Illaroo (-29.72, 153.30; 9.2 km) and each of these beaches was split into two zones (north and south) of similar size to simulate the management zoning of the commercially fished beaches. All beaches are characteristically fronted by bar and rip systems and exposed to a wide range of ocean conditions (Short, 2007).

Sampling of clams was stratified temporally across three distinct periods, before and during the six-month austral winter-spring (1 June to 30 November) commercial harvesting season for clams in 2013. This was 3 years after the spatial fishing closures, and 1 year after the six-month temporal fishing closure and the size and trip limit restrictions were implemented. The length of each sampling period and the interval between consecutive sampling periods was six weeks. The 'Before' sampling was in April/May when all beaches were totally closed to commercial clam harvesting, the 'Early' harvesting in July/August and 'Late' harvesting in October/November, with sampling beginning 6 and 18 weeks, respectively, after the commencement of the harvesting season. In each of these three periods, sampling was further stratified across two randomly selected days in each of three randomly selected weeks to account for short-term variability in clam densities (Gray, 2016).

Sampling was also stratified spatially across two habitats, the swash zone and the dry sand belt typically located 10–30 m above the swash zone at low tide. To account for small-scale spatial variability (Gray, 2016), on each sampling day, four locations in the swash zone and another four locations in the dry sand clam belt were selected at random within each commercially fished and non-fished zone on each commercially fished beach, and in each simulated zone on each control

beach. At each of these locations, six replicate samples were taken so that a total of 96 samples were collected each day of sampling on each beach. Sampling was done during daytime within 3 h either side of low tide (Gray, 2016). It took approximately 4 h to complete sampling each day and the order in which each zone was sampled was randomly determined each day.

Different sampling gears and methods were used to sample clams in each habitat. Clams in the swash zone were sampled by finger digging for 30 s a small area (average diameter 57 cm, depth 18 cm) of sand and scooping it into a net that had 12 mm mesh hung on a frame measuring 35×21 cm (Gray et al., 2014). Clams in the dry sand were sampled by excavating sand to a depth of 20 cm within a square box quadrat that had 32 cm sides (James and Fairweather, 1995). The excavated sand was sieved through a net with 6 mm mesh. All clams collected in each replicate sample were counted and measured for shell length (SL, mm) and operational information including time of sampling and beach and sea conditions were recorded.

2.2. Data analyses

For each beach, differences between zones in the densities of clams across the 3 harvesting periods were tested using five-factor nonparametric permutational analyses of variance (PERMANOVA; Anderson, 2001). The analytical design had the factors: Zone (fixed), Period (fixed), Week (nested in period—random), Day (nested in week and period—random), Site (nested in zone, day, week and period—random). Separate analyses were done for each habitat (swash and dry sand) on each beach because they were sampled in different ways. Separate analyses were done on the densities of total, legal (\geq 45 mm SL) and sublegal (<45 mm SL) sized clams. Each univariate analysis was based on the Euclidean distance measure and Type III (partial) sums of squares were calculated using 999 unrestricted permutations of the raw data. The proportion of variation attributable to each factor and interaction in each model was calculated to aid interpretation of the results. All negative variation component values were treated as zero, eliminated from the analysis and the remaining variation components recalculated (Fletcher and Underwood, 2002). Each component directly estimated variability for each term independent of the other terms. All analyses were done using the PRIMER 6 and PERMANOVA⁺ programs (Anderson et al., 2008).

PERMANOVA was also used to test whether the size compositions of sampled populations of clams differed between zones and periods. The proportion of clams in each 5 mm SL class was used to classify samples. Because, clams were not sampled in large densities across all replicate locations and days within each week, the two samples taken in each week were pooled for each zone separately to provide a total of three replicate size compositions at the level of week for each sampling period and zone. Thus, the two factor analytical design for each analysis was: Zone and Period (both fixed). Separate analyses were done for the dry and swash habitats on each beach and each analysis was based on the Bray Curtis dissimilarity matrix with Type III (partial) sums-of-squares calculated using 999 unrestricted permutations of residuals under a reduced model.

3. Results

3.1. Densities of clams

For the two commercially fished beaches there was no significant zone \times period effect in any analysis (PERMANOVA, *P-perm* > 0.05, Table 1), indicating there were no detectable large-scale effects of commercial harvesting on densities of clams from before to during (early and late) the harvesting season. The densities of total and legal clams in the dry on South Ballina differed significantly between zones, but these were consistent across periods (Table 1, Fig. 1). Potential short-term fishing effects were identified as: (1) significant zone \times week interactions in the densities of clams in the swash on South Ballina, and (2) significant zone \times day interactions for the densities of clams in the dry habitat across both habitats (except for sublegal clams in the swash) on Stockton and in the dry on South Ballina (Table 1). Although most pairwise comparisons were limited in power (low number of available permutations) to detect specific differences spatio-temporal differences in densities, they identified that: (1) clams in the swash habitat occurred in lower densities in the non-fished zone on South Ballina across weeks 1 and 7 (Fig. 1); (2) densities of total and legal clams were significantly lower in the non-fished zone in the dry habitat on South Ballina on days 2, 8, 9 and 12, and Stockton on day 7, as well as in the swash on Stockton on days 2, 12 and 13 (Fig. 1), and (3) densities of total and legal clams were significantly lower in the commercially fished zone in the dry habitat on Stockton on days 4 and 17 and in the swash on day 1 (Fig. 1).

For the control beaches, the densities of total and legal clams in the dry were greater in the northern zone on Sandon throughout sampling (PERMANOVA, *P-perm* < 0.05, Table 1, Fig. 2). There were significant zone × period interactions for total and sublegal clams and zone × day interactions for total and legal clams in the swash on Sandon (Table 1). The densities of total and legal clams also differed according to the zone × day interaction in the swash and sublegal clams in the dry on Sandon. The pairwise comparisons identified that densities of total and legal clams in the swash were significantly greater in the northern zone on days 14, 15 and 17 (Fig. 2). There were no significant zone or zone × time interactions for any density parameter in either habitat on Illaroo (Table 1, Fig. 2).

The densities of clams across some beaches also significantly differed according to harvesting period, but these were consistent across zones (i.e. non-significant zone \times period interactions, Table 1). The pairwise tests indicated that densities of total clams were significantly lower in the: (1) late harvest period than in the before and early periods in the dry on South Ballina (Fig. 1), and (2) early compared to the before and late periods in the swash on Illaroo (Fig. 2).

Table 1

Results of PERMANOVAs comparing densities of total, legal and sublegal sized clams across commercially fished and non-fished zones on South Ballina and Stockton beaches, and across zones on the control beaches of Sandon and Illaroo. Bold and shaded terms are those that if significant might signify a possible effect of management zoning and fishing impact across the commercially fished beaches.

Commercially-fished beaches	df	Swash habitat			df	Dry habitat		
		Total	Legal	Sublegal		Total	Legal	Sublega
South Ballina beach								
Zone	1	ns	ns	ns	1	**	**	ns
Period	2	**	ns	•	2			
Week(Period) Zone × Period	6 2	ns	ns	ns	6 2	20	20	
		ns	ns	ns		ns •	ns	ns
Day(Week(Period))	9	ns	ns *	ns	9			ns
Zone ×Week(Period)	6	ns			6	ns	ns	ns **
Zone × Day(Week(Period))	9	ns	ns	ns	9			
Site(Zone \times Day(Week(Period)))	108	***	***	***	108	***	***	***
Residual	720				720			
Stockton beach								
Zone	1	ns	ns	ns	1	ns	ns	ns
Period	2	ns	ns	ns	2	ns	ns	ns
Week(Period)	6				6			
Zone $ imes$ Period	2	ns	ns	ns	2	ns	ns	ns
Day(Week(Period))	9	ns	***	ns	9	**	**	ns
Zone ×Week(Period)	6	ns	ns	ns	6	ns	ns	ns
$Zone \times Day(Week(Period))$	9	***	**	**	9		**	ns
Site(Zone \times Day(Week(Period)))	108	***	***	***	108	***	***	***
Residual	720				720			
Control beaches	df	Swash habitat			df	df Dry habitat		
		Total	Legal	Sublegal		Total	Legal	Sublega
Sandon beach		**		***		**	**	**
Zone	1			**	1			
Period Week(Period)	2 5	ns	ns ns	ns	2 6	ns ns	ns ns	ns ns
Zone × Period	2	**	ns	**	2	ns	ns	ns
Day(Week(Period))	8	***	***		9	*	*	
Zone ×Week(Period)	5	ns	ns	ns	6	ns	ns	ns
Zone \times Day(Week(Period))	8	***	***	ns	9	ns	ns	*
		***	•••	***		***	***	
Site(Zone × Day(Week(Period))) Residual	96 640				108 720			
Residudi	040				720			
Illaroo beach								
Zone	1	ns	ns	ns	1	ns *	ns *	ns
Period Week(Period)	2 5	ns	ns	ns	2 6		ns	
Zone × Period	2	ns	ns	ns	2	ns	ns	ns
Day(Week(Period))	8	**	**	**	9	ns	ns	ns
Zone ×Week(Period)		nc	nc	nc				
	5	ns	ns	ns	6	ns	ns	ns
Zone × Day(Week(Period))	8	ns	ns	ns	9	ns	ns	ns
	96	***	***	***	108	***	***	***
Site(Zone × Day(Week(Period))) Residual	96 640				720			

df = degrees of freedom, ns = P-perm > 0.05.

* P-perm < 0.05. ** P-perm < 0.01. *** P-perm < 0.01.

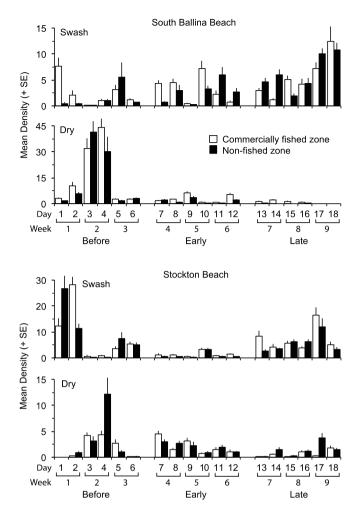


Fig. 1. Mean (+ SE) densities of *Donax deltoides* sampled in the swash and dry habitats across the commercially fished and non-fished zones on South Ballina and Stockton beaches before, early and late harvesting 2013.

The densities of clams across both habitats and all four beaches consistently differed in a significant manner at the smallest scale of sampling (i.e. across sites sampled each day in each zone, Table 1). Moreover, the components of variation in all density analyses were greatest in 22 of 24 analyses for the residual (i.e. among replicate samples), accounting for 30%-71% of total variation in each analysis. The factor site contributed the second largest component of variation in 14 of 24 analyses (4%–36%). These combined results highlight the dominance of small-scale spatio-temporal patchiness in clams across all beaches. The contribution to total variation was also high for Period on South Ballina (6%–20%) and Illaroo (9%–15%), and for week on South Ballina (5%–37%) and Stockton (9%–24%). Zone contributed <2% of variation across all beaches except Sandon where it accounted for 6%–11% of variation.

3.2. Size compositions of clams

Across both habitats there were no significant differences in the size compositions of clams between zones on the commercially fished or the control beaches, before or during the harvesting season (PERMANOVA, P > 0.05, Table 2, Figs. 3 and 4). In contrast, significant differences in size compositions were evident among some sampling periods, but these were the same across the two zones on each beach (i.e. non-significant Zone × Period interactions, Table 2). These combined results indicated that commercial fishing did not significantly impact size compositions of clams.

There was a general trend across both habitats on each beach for a greater proportion of small (5–20 mm) clams in size compositions in the early and late harvest periods compared to before harvesting (Figs. 3 and 4). The predominant exception being South Ballina, where small clams were only apparent late harvesting. On each beach, the size compositions of clams were generally similar across both habitats within each sampling period.

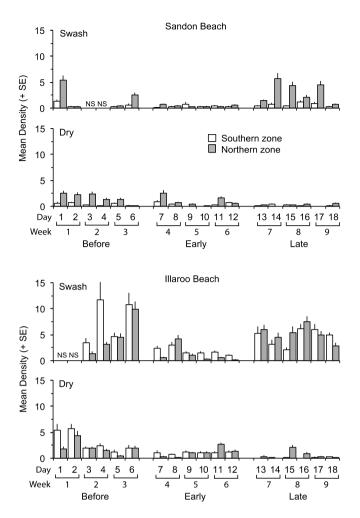


Fig. 2. Mean (+ SE) densities of *Donax deltoides* sampled in the swash and dry habitats across the two non-fished zones on Sandon and Illaroo beaches before, early and late harvesting 2013. NS = not sampled.

Table 2

Summary results of PERMANOVA and subsequent pairwise tests comparing the size compositions of clams across zones and harvest periods in the swash and dry habitats on each fished and control beach.

Source of variation	df	Commercially fished beaches						
		South Ballina Swash	South Ballina Dry	Stockton Swash	Stockton Dry			
Zone Period Zone × Period	1, 12 2, 12 2, 12	ns 	ns **	ns ns ns	ns **			
Pairwise period	2, 12	$B = E, B \neq L, E \neq L$	$B \neq E, B \neq L, E \neq L$	115	$B \neq E, B \neq L, E = L$			
Source of variation	df	Control beaches						
		Sandon Swash	Sandon Dry	Illaroo Swash	Illaroo Dry			
Zone Period Zone × Period	1, 12 2, 12 2, 12	ns **	ns ns ns	ns **	ns ns ns			
Pairwise period	2, 12	$B \neq E, B = L, E \neq L$		$B \neq E, B \neq L, E \neq L$				

df = degrees of freedom, B = before, E = early, L = late harvest, ns = P-perm > 0.05.

** *P*-perm < 0.01.

** P-perm < 0.001.

South Ballina Beach

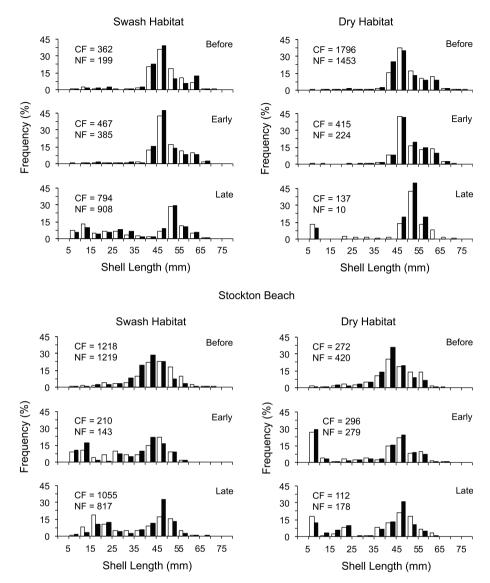


Fig. 3. Size compositions of *Donax deltoides* sampled in the swash and dry habitats across the commercially fished and non-fished zones of South Ballina and Stockton beaches before, early and late harvesting 2013. Sample sizes are shown on each graph. Shading as in Fig. 1; CF = commercially fished zone, NF = non-fished zone.

4. Discussion

For the commercially fished beaches, there were no significant zone-related differences in densities of clams in either the swash or dry habitats greater than the level of week, indicating that the potential effects of commercial harvesting on clam densities were highly variable and ephemeral, being dependent on the particular day or week sampled. This occurred even though during the 6-month fishing season approximately 10400 and 5700 kg of clams were harvested from South Ballina and Stockton beaches, respectively. It is unlikely that the harvesting of clams by recreational and indigenous fishers impacted the results obtained here. Relatively few non-commercial fishers were observed harvesting clams in either the commercially fished or non-fished zones throughout the study, and although their total harvests are unknown, it probably was considerably less than reported total commercial harvests across each beach (Murray-Jones and Steffe, 2000). It is also unlikely that commercial harvesters extensively worked the non-fished zones on either beach due to a combination of strong industry codes, local community awareness and fisheries compliance.

Significant spatio-temporal interactions (zone \times period and zone \times day) in clam densities were also evident in the swash habitat across one control beach: Sandon. Moreover, densities of clams in the dry habitat on Sandon differed between zones in a consistent manner across all periods. These combined results demonstrate that densities of clams can naturally

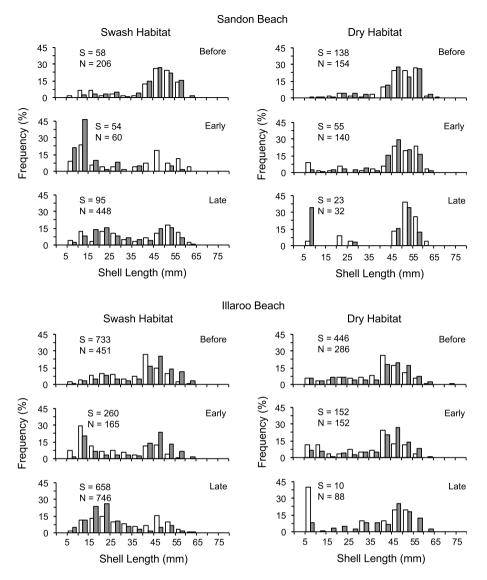


Fig. 4. Size compositions of *Donax deltoides* sampled in the swash and dry habitats across the two non-fished zones of Sandon and Illaroo beaches before, early and late harvesting 2013. Sample sizes are shown on each graph. Shading as in Fig. 2; S = southern zone, N = northern zone.

fluctuate between designated zones or sections along beaches across short (days) and longer (months) temporal scales. Whilst the reasons for this are not apparent here, it means that the observed zone \times time interactions on the commercially fished beaches may have been the result of natural processes unrelated to commercial fishing. Delineating between these alternate hypotheses is difficult, especially given that densities of clams across both habitats were often lower in the non-fished zones than the commercially fished zones, and that such interactions occurred before and during harvesting. Many such interactions, therefore, were probably pulse responses (Underwood, 1989) of clams to natural small-scale stochastic processes, such as local changes in wave or beach conditions, operating independently in the different zones along each beach (McLachlan and Hesp, 1984).

In contrast to densities, the size compositions of clams across both habitats did not significantly differ between zones on either the fished or control beaches, but this was only assessed at the scale of period due to sample size considerations. Although greater proportions of sublegal clams were present in the early and late compared to the before harvest period, this was consistent across both zones on each beach and due to the recruitment of small (10–20 mm SL) clams, and not the result of truncation of larger animals (i.e. due to harvesting). This austral winter/spring timing of recruitment of small clams concurs with reported spawning periods (Ferguson and Ward, 2014).

Current restrictions on commercial fishing may have dampened the detection of longer-term harvesting impacts and concomitant differences between management zones in densities and sizes of clams. Commercial fishers can often harvest 40 kg of clams across a relatively small stretch of swash habitat (<100 m), and from a small area (<50 m²) of dry habitat, in <1 h (unpublished data). Thus, the immediate (and cumulative total fishing season) environmental footprint left by this

scale of harvesting may not be broad enough to be detected across large spatio-temporal scales. It is hypothesized that under current management arrangements, fishing-related impacts may only manifest across local spatial and temporal scales on a beach. For example, the few instances when clam densities were lower in the commercially fished zone (e.g. days 14 and 17 in the dry on Stockton) may have resulted from commercial fishers (coincidentally) harvesting clams at the actual sampling sites (as opposed to the general vicinity) shortly before (e.g. previous tide or day) sampling occurred. Whilst this cannot be tested here, sampling across small scales immediately before and after actual harvesting events could potential identify the extent and longevity of localized fishing-related impacts on clams (Carvalho et al., 2013).

Beach clams are mobile organisms that actively move along and across beaches depending on ocean and beach conditions (Leber, 1982; Ellers, 1995; Dugan and McLachlan, 1999), with large seas and storm events also potentially redistributing clams across each spatial dimension. It is reasonable to assume that individual clams may have actively migrated between management zones on each fished beach, thereby masking detection of any potential longer-term zone-related differences in densities and size compositions. Quantifying the extent and the mechanisms that drive the translocation of clams along and across beaches is an important avenue of research that will assist in determining the value of closed fishing zones and their potential conservation benefits.

The lack of significant longer-term impacts (i.e. $zone \times period$) on the densities and sizes of clams does not imply commercial harvesting at the levels reported here has no impact on populations, and similarly that the zones closed to commercial fishing do not provide conservation benefits to clams. Indeed, like other no- and partial-take fishing closures, the non-fished zones may provide necessary (albeit even temporary) refuge to a proportion of the total clam population on each beach, potentially alleviating population-wide impacts of commercial harvesting (Gell and Roberts, 2003; Botsford et al., 2009). The non-fished zones sampled here represented <20% of available habitat on each beach, and more research is required to determine whether this is adequate for sustainability purposes (Halpern, 2003). However, many east Australian beaches are now totally closed to clam harvesting and the total area that is protected across all beaches, as well as the actual area on beaches that fishers actively utilize for harvesting, needs to be considered in the overall management of the resource. In particular, the broader ecological effects of alternate levels of protective areas and harvesting on total reproductive output (Brazeiro and Defeo, 1999) and linkages with recruitment need to be assessed. Moreover, the potential impacts of clam harvesting on other beach organisms and ecosystem functioning are required for a more holistic approach to protective zoning strategies and the overall management of sandy beaches.

The zoning of beaches into commercially fished and non-fished zones was in part implemented to alleviate social conflicts among different beach user groups. Although the success of this objective was not assessed here, it needs to be addressed as it is imperative that management initiatives whether they are for social, economic or biological reasons be tested (Underwood, 1995). Such knowledge will ultimately help determine the broader applicability of such strategies for managing social issues on sandy beaches (Charles and Wilson, 2009; McLachlan et al., 2013).

This study was the first experiment to test for the effects of an implemented fisheries spatial management strategy on beach clams in eastern Australia, and among the few done globally (Defeo et al., 2009). In doing so, it highlighted the difficulties in determining potential impacts of fishing and the subsequent value of spatial fishing closures on clams, particularly given the current levels of commercial harvests in the study fishery. Nevertheless, the study demonstrated the necessity of incorporating appropriate external controls (i.e. the non-fished beaches) in evaluating management strategies, as well as the value of hierarchical sampling schemes that allow for response measures of potential impacts across different spatial and temporal scales. Such measures are not only important for management, but for assessing the relevant scales of ecological processes and their subsequent influences on assemblages (Underwood et al., 2000; Gray, 2016). Along with a greater understanding of the spatial dynamics and connectivity of clams along and among beaches, further experimental studies are required to evaluate other aspects of management initiatives concerning clam fisheries, including temporal closures, quotas and legal size restrictions. Such information will help assess the global applicability of alternate management initiatives for sustainable clam harvesting, and contribute towards the greater conservation and management of sandy beach ecosystems.

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