






## ARTICLE

# Lack of population structure in an important fishery species of mud shrimp, *Trypaea australiensis*

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## Abstract

From a conservation standpoint, species that are managed without consideration of their population sizes and connectivity have the potential to be over-exploited and/or incur population decline. The burrowing shrimp, *Trypaea australiensis*, is an important ecosystem engineer and fishery resource caught in large numbers for which population information is unknown for properly managing the species. Here, we determined the level of population structure of *T. australiensis* across three locations along the East Coast of New South Wales, Australia, using genome-wide single nucleotide polymorphisms (SNPs) obtained through double digest Restriction-site Associated DNA-sequencing (ddRAD-seq). Analysis of population structure, including pairwise  $F_{st}$  (-0.003 to -0.001), STRUCTURE ( $K=2$ ) and Discriminant Analysis of Principal Components (DAPC) showed no evidence of structure among locations. Our findings provide crucial preliminary population genetic data for a key cryptic species, that also suggests gene flow among sampling locations enables the management of fisheries throughout the study area as a single unit.

## KEYWORDS

crustaceans, cryptic species, estuaries, genetics, invertebrates

## 1 | INTRODUCTION

Dispersal strategies of aquatic organisms vary considerably within and among populations and often depend on life history and environmental barriers (Cowen & Sponaugle, 2009; DiBacco & Levin, 2000; Fobert et al., 2019; McEdward, 1995; Mileikovsky, 1971; Palumbi, 1994). Many marine species are “site-attached” during the adult life stage and rely on a planktonic larval stage for dispersal (DiBacco & Levin, 2000; Siegel et al., 2008; Thorpe et al., 2000). Environmental barriers, such as low energy

oceanic currents and tides, degree of geographic separation, and availability of suitable settlement locations, affect the extent to which larvae disperse to connect geographically separate populations (Cowen & Sponaugle, 2009; Giangrande et al., 2017; Treml et al., 2012; van der Meer et al., 2012; Waters et al., 2014). Therefore, to ensure appropriate management of populations and species, the degree of population connectivity must be quantified to reveal changes in population structure over time (Bohonak, 1999; Brooker et al., 2000; Gawarkiewicz et al., 2007; McMillen-Jackson & Bert, 2004).

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Site-attached marine species often have a limited reproductive capacity to replenish their populations, so their exploitation as an economic resource by commercial and recreational fisheries is of particular concern (Contessa & Bird, 2004; McPhee et al., 2002; Moschetto et al., 2020; Thorpe et al., 2000). Catch rates for these species (e.g. bivalves, sea urchins, crustaceans and gastropods) have increased significantly in recent years, with over-exploitation threatening population stability (Chick, 2021; Contessa & Bird, 2004; McPhee et al., 2002; Rotherham, 2004; Skilleter et al., 2005; Thorpe et al., 2000). Interest in the management and regulation of invertebrate fisheries is limited, so many continue to be harvested without adequate management strategies (King, 1995; Koljonen, 2001). Lack of appropriate management can result in unforeseen consequences for species, populations and the ecosystem, particularly if a species has a prominent role in modifying the environment as “ecosystem engineers” (Castorani et al., 2014; Coleman & Williams, 2002; Moore, 2006; Pascal et al., 2019). To address gaps in marine species management, population connectivity and species dispersal have been studied to identify populations at risk (Nims et al., 2008; Palumbi, 2003; von der Heyden, 2009; Weersing & Toonen, 2009). By coupling knowledge of population genetic structure with ecology and life history of species, management strategies can be better informed to ensure sustainable use of key invertebrate species (Gaylord et al., 2005; Koljonen, 2001).

An important yet understudied ecosystem engineer is the burrowing mud shrimp, *Trypaea australiensis*, that is endemic to the East coast of Australia from upper Queensland down to Victoria and South Australia and supports important fisheries (Butler et al., 2009; Hailstone & Stephenson, 1961; Rotherham, 2004). The life cycle of *T. australiensis* typically begins with production of one to five broods during warm months of the year (Hailstone & Stephenson, 1961; Rotherham & West, 2007). Fertilised broods hatch as planktonic larvae that disperse to other areas where they settle into uninhabited burrows. Larval duration ranges from 2 weeks (Butler et al., 2009) to 6 weeks (Hailstone & Stephenson, 1961; Rotherham & West, 2007), and their average lifespan is 3–4 years (Hailstone & Stephenson, 1961). Dispersal distance and population genetic structure are unknown for *T. australiensis*, although population structure has been investigated for the related species *Callichirus major*, *Callichirus islagrande* and *Lepidophthalmus* sp. (Nates et al., 1997; Staton & Felder, 1995). *T. australiensis* has the potential to exhibit high connectivity (open) among populations (Chick, 2021; Cowen et al., 2000; Staton et al., 2000; Staton & Felder, 1995; Strathmann et al., 2002) because larval duration before settlement is relatively long (Hailstone & Stephenson, 1961; Rotherham & West, 2007) and oceanic currents are extensive along the East Coast of Australia (Cetina-Heredia et al., 2015; Everett et al., 2017). However, local processes within the habitat of this species, such as tidal fluctuations within low-energy estuaries and coastal topography constraints, may act as environmental barriers that could limit dispersal of these small shrimp and cause distinction among

populations or even create closed populations (Silva et al., 2019; Waters et al., 2014; White et al., 2010).

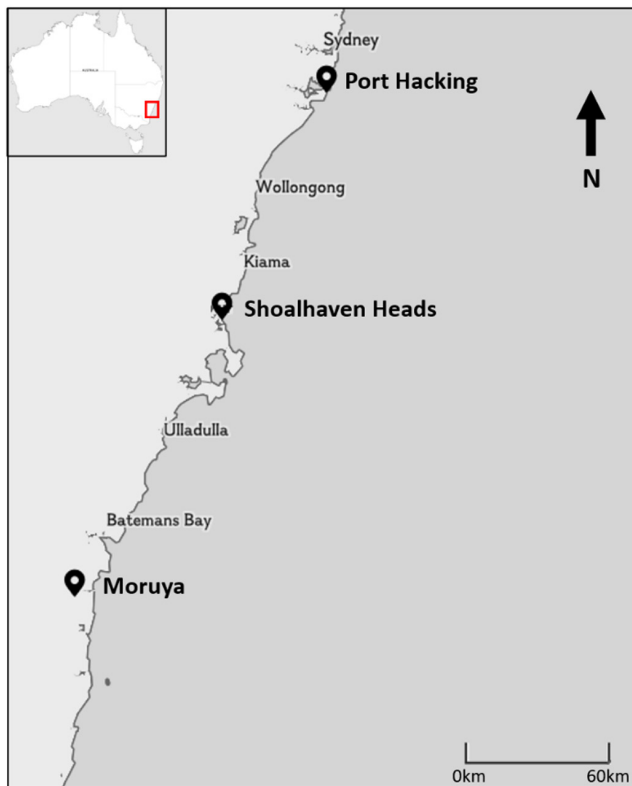
As a fundamental ecosystem engineer on Australian mud flats (Butler & Bird, 2008; Katrak & Bird, 2003) *T. australiensis* indirectly influences abundance of coexisting species such as bivalves, sea-grasses, algae and benthic fish (Berkenbusch & Rowden, 2003; Pillay & Branch, 2011; Pinnegar et al., 2000; Rotherham, 2004). The species is also an important economic and social commodity in commercial and recreational fisheries, as a common bait for anglers (Contessa & Bird, 2004; McPhee et al., 2002; Rotherham, 2004). Because of its importance to the ecosystem and anglers, the degree of population connectivity and genetic structure of this species must be understood to maintain population health. Before 2010, no catch limits were in place for *T. australiensis* and populations were classified as “moderately fished” by the New South Wales Department of Primary Industries (DPI) (Chick, 2021; Rotherham, 2004), which indicates that the species was fished in most of its range and that fishing resulted in less than 50% of the species dying from natural causes (Stewart, 2017). Since 2010, bag limits have been placed on recreational (100 shrimp per angler trip) and commercial (5.6 tonnes total) fisheries (Chick, 2021). The latest (2020–2021) stock assessment stated that *T. australiensis* was classified as “sustainable,” although the report acknowledged that population dynamics could have been underestimated (Chick, 2021). Population estimates were largely based on one location with inconsistent sampling periods that limited its applicability to the entire range of the species. Therefore, to inform effective management, a wider geographic area should be sampled to ensure populations can be delimited if present.

To quantify the degree of connectivity of *T. australiensis* along the New South Wales coast in Australia, we used a genomic approach to compare population structure at three locations often targeted for collections. Given the potential for larval dispersal by the East Australian Current (EAC) (Chick, 2021; Hailstone & Stephenson, 1961; Rotherham, 2004; Silva et al., 2019), we hypothesised that local populations would exhibit little population structure. Results could provide a preliminary assessment of this species population structure and connectivity.

## 2 | METHODS

### 2.1 | Sample sites and collection

The study area included three locations along the East Coast of New South Wales Australia: Port Hacking, Shoalhaven Heads and Moruya, between September 2018 to August 2019. Sampling sites were spread over ~250 km, with ~120 km between Port Hacking and Shoalhaven Heads and ~130 km between Shoalhaven Heads and Moruya (Figure 1). Sites were chosen to ensure that: (i) shrimp were collected in areas open to fishing (no collections in no-take zones or protected areas); (ii) similar methods were used at each site (similar-sized mudflats enabling collection along the low to mid tide area



**FIGURE 1** Location of three sampling locations for the burrowing mud shrimp *Trypaea australiensis* along the East Coast of New South Wales, Australia between September 2018 and August 2019. Port Hacking (34°04'37.2"S 151°07'49.8"E), Shoalhaven Heads (34°51'27.4"S 150°44'52.1"E), Moruya (35°54'23.0"S 150°07'49.8"E).

2–3 hrs before low tide); and (iii) site access and sampling were not obstructed by high and low tidal changes.

DNA was collected from shrimp that were suctioned from their burrows using a standard 30-inch nipper pump (Wilson, Brisbane, QLD, Australia). Scissors were used to collect tissue from the last pair of pleopods on shrimp and then preserved in 80% ethanol. Samples were taken from all individuals suctioned from a single burrow when more than one individual was collected. Fifty-three *T. australiensis* were sampled from each site for population genetic analysis, totalling 159 specimens (Table S1).

## 2.2 | DNA extraction and genotyping

Genomic DNA was extracted with a Wizard Genomic DNA Purification Kit (Promega, Madison, WI, USA) using manufacturer protocol and quantified using a NanoDrop 2000c (Thermo Scientific, Waltham, MA, USA). Samples were processed using the ddRAD (double digest restriction-site associated digest) library preparation protocol (Peterson et al., 2012). Restriction enzymes EcoRI and NlaIII were used to digest libraries, which were barcoded and pooled. Pools were size selected using a Blue Pippin (Sage Science, Beverly, MA, USA) to obtain 280–375 bp fragments, then tagged

with indexed primers and amplified using PCR. Libraries were sequenced on a NextSeq 500 to yield 2 × 150 bp sequences (Illumina, San Diego, CA, USA).

## 2.3 | Data analysis

### 2.3.1 | SNP filtering

Initial quality control and demultiplexing were completed using STACKS v.2.3d software (Catchen et al., 2011, 2013), and sequences were only retained with exact barcodes before trimming to 150 bp. Next, we used STACKS v.2.54 following Rochette et al. (2019) to assemble loci and call Single Nucleotide Polymorphisms (SNPs). Settings for the Denovo pipeline included three for the distance between stacks (-M), the distance between catalogue loci (-n) and two for the minimum stack depth of coverage (-m). Poor-quality samples with less than 50% of loci were excluded from further analysis, which left a final set of 125 samples (Supplementary Table S1). Within STACKS, the “populations” function was used to export loci that were called in >80% of samples (-r), present in all three populations (-p), had observed heterozygosity less than 0.7 (--max-obs-het), and met a minimum minor allele count of 2 (--min-mac). Loci were removed if significantly out of Hardy–Weinberg Equilibrium (HWE) in two or more sampling locations. To calculate divergence from Hardy–Weinberg equilibrium for each locus, the Hardy–Weinberg (--hwe) function was used in STACKS, and *p*-values were adjusted for False Discovery Rate with the “BY” correction of the “p.adjust” function in R v3.6.3 (Rstudio V1.4.1106) and RStudio (R Core Team, 2020; RStudio Team, 2021). The final set of loci was exported using the --write-single-snp option to avoid closely linked SNPs.

### 2.3.2 | Population structure

To quantify population structure among sampled populations, Arlequin v3.5.2.2 (Excoffier & Lischer, 2010) was used for analysis of molecular variance (AMOVA) with 30,000 permutations and to assess hierarchical population structure among field sites using pairwise  $F_{ST}$  values. Genetic diversity statistics are estimated using the “basic.stats” function in the R package hierfstat (Goudet, 2005) included observed heterozygosity ( $H_o$ ), expected heterozygosity ( $H_e$ ) and inbreeding coefficient ( $F_{is}$ ).

STRUCTURE v.2.3.4 (Pritchard et al., 2000) was used to identify patterns of admixture in the mud shrimp population based on SNP data. Settings included 100,000 iterations for burn-in and 500,000 iterations of Markov-chain Monte Carlo (MCMC), with nine independent runs completed on each of *K* values (*K*=1–4). The most likely *K* value was determined through STRUCTURE HARVESTER (Earl & vonHoldt, 2012) applying the  $\Delta K$  Evanno method (Evanno et al., 2005) (Figure S1). STRUCTURE graphs were produced in R using data from the Cluster Markov Packager Across Ks (CLUMPAK) online tool (Kopelman et al., 2015). A Discriminant Analysis of Principal



Components (DAPC) was conducted with the R package adegenet v1.7–16 (Jombart, 2008; Jombart & Ahmed, 2011) for a dataset with missing data replaced by the mean allele frequency for each locus using the “scaleGen” function. After analysing cross-validation results from the function “xval.dapc,” two discriminant functions and three principal components were retained for the DAPC.  $K$  values were found using the “find.clusters” function, which uses a k-means approach to identify genetic clusters, and the Bayesian Information Criterion (BIC) to determine the most likely  $K$  value (Figure S2).

### 3 | RESULTS

For the final sample of 125 burrowing mud shrimp, 1809 loci were variable after filtering. Among the three sampled populations, the observed heterozygosity was  $H_o=0.0404$ , the expected heterozygosity was  $H_e=0.0471$  and the inbreeding coefficient was  $F_{is}=0.0037$ . Population structure was not evident among the three sampling sites ( $F_{ST}=-0.00266$ ,  $p=0.840$ ), and pairwise  $F_{ST}$  between sampling sites did not differ significantly (Table 1).

Two patterns of admixture were evident among the three sample sites, based on Bayesian cluster analysis (STRUCTURE) and DAPC analysis (Figures 2 and 3, Figure S1). Differentiation among individuals was slight and not defined by sampling location (Figures 2 and 3). All individuals had most of their ancestry from one cluster (Figure 2, blue colour), while 26 individuals across all three sites had another cluster of alleles (Figure 2, red colour) when the number of clusters was set to more than two, which is also reflected along Linear Discriminant 1 in the DAPC (Figure 3).

### 4 | DISCUSSION

We found evidence of shared genes and gene flow between three locations of *Trypaea australiensis* over approximately 250 km of the east coast of New South Wales, Australia. This lack of genetic structure is consistent with studies of the other shrimp species *Neotrypaea californiensis* and *Farfantepenaeus duorarum* (Kozuka, 2008; McMillen-Jackson & Bert, 2004). Our sampling locations were closer together (maximum 250 km between sites) than those sampled by McMillen-Jackson and Bert (2004; 1500 km between sites) and farther apart than those sampled by Kozuka (2008; 90 km between sites). Because

TABLE 1 Pairwise  $F_{ST}$  values (upper cells) and  $p$ -values (lower cells) of the burrowing mud shrimp *Trypaea australiensis* among three sampling sites along the East Coast of New South Wales, Australia between September 2018 and August 2019.

	Port hacking ( $N=50$ )	Shoalhaven heads ( $N=25$ )	Moruya ( $N=49$ )
Port Hacking		$0.85 \pm 0.039$	$0.91 \pm 0.025$
Shoalhaven Heads	$-0.00336$		$0.36 \pm 0.041$
Moruya	$-0.00292$	$-0.00125$	

of distances among our sampling locations, and the length of larval development (Hailstone & Stephenson, 1961; Nates et al., 1997), we expected *T. australiensis* larvae to be able to disperse to other estuaries on local and oceanic currents (Selkoe & Toonen, 2011; Weersing & Toonen, 2009). The East Australian Current can support dispersal stretching the length of the east coast of Australia (Everett et al., 2017; Waters et al., 2014) and would facilitate larval transport from northern to southern populations, with local tides facilitating the movement of larvae into adjacent estuarine habitats (Everett et al., 2017; Waters et al., 2014).

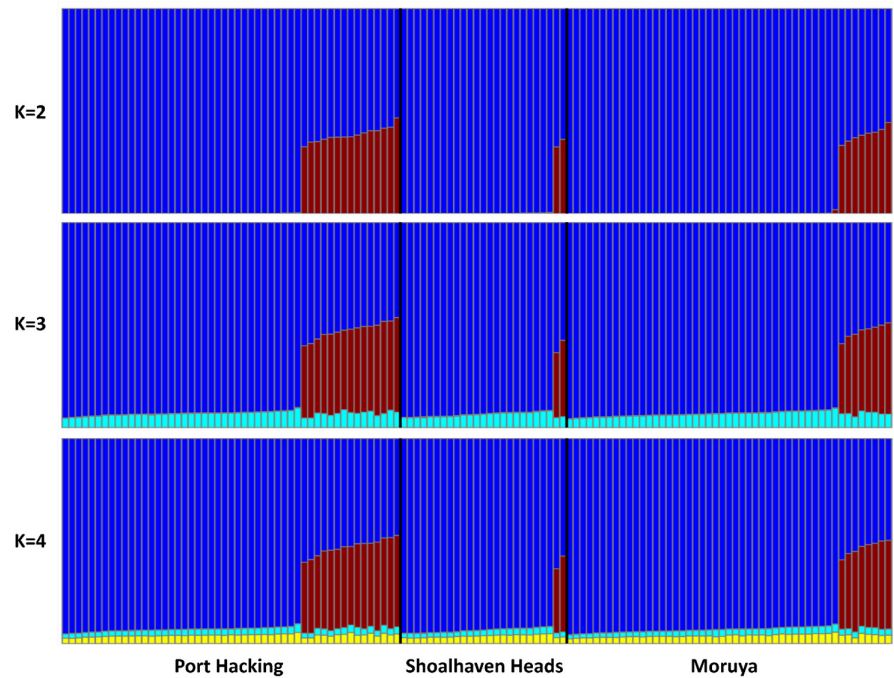
The two slight patterns of admixture we identified, particularly the secondary clustering of shared alleles for a portion of sampled individuals (with representative samples from each of the three locations), may have resulted from our sampling range. Meaning that samples were collected by chance from the admixture zone for two larger populations as well as the core of only one of those populations thereby creating this slight difference in shared alleles (Lessios et al., 2003; Palumbi et al., 1997). However, further studies over a larger geographical range and a study of biological (larval dispersal distances) and environmental (tidal fluctuations and oceanic currents) factors would be needed to determine if two larger populations contribute to gene flow (Palumbi et al., 1997).

The low level of heterozygosity we found (i.e. low genetic diversity and nearly no inbreeding) suggested a large randomly mating population of *T. australiensis* along a 250-km stretch of the East Coast of NSW that could be managed as a single population. Whereby conserving the population at one location will benefit the others through gene flow among locations (Dumbauld & Bosley, 2018; Fogarty & Botsford, 2006; Sanvicente-Añorve et al., 2018). However, high catch rates could still cause over-exploitation of the fishery (Chick, 2021; Rotherham, 2004), which would ultimately reduce population sizes across the geographic range through time (Thorpe et al., 2000). Little is known about the effects of bait fishing, but recreational fishery catch rates of *T. australiensis* have been increasing (Chick, 2021), with 700,800 taken in 2017–2018 (Murphy et al., 2020) and 823,391 in 2019–2020 (Murphy et al., 2022). In the 2021 stock assessment, catch rates were likely underestimated due to survey methods and the inclusion of few estuarine locations (Chick, 2021). If fishing mortality is depleting populations of *T. australiensis*, particularly in any source locations, then additional restrictions may be needed despite gene flow. Future studies should evaluate if current fishing mortality is sustainable for the panmictic population that stretches over our 250-km study area.

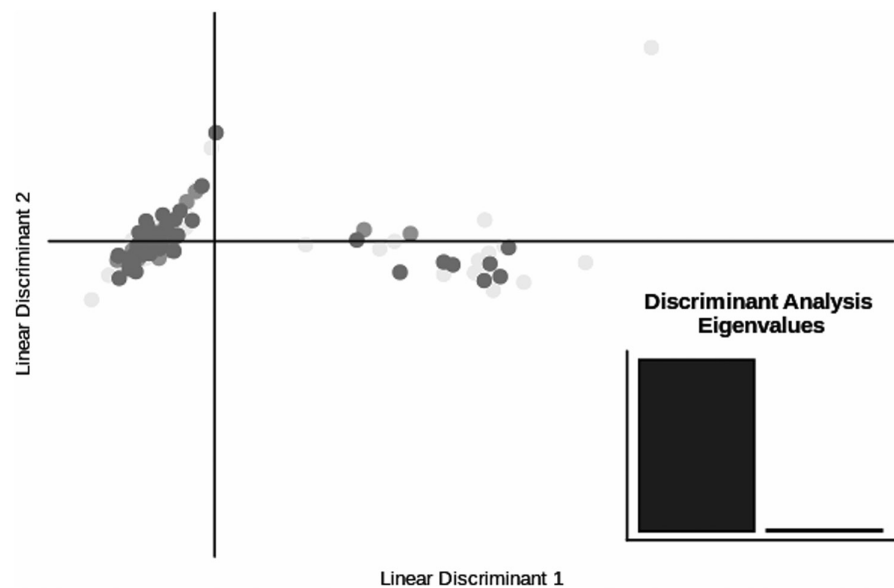
Our study provides the necessary baseline data for designing future population genetic studies. Further, it is evident that studies involving species with similar life history and dispersal patterns as these shrimp require a holistic approach towards management assessments. It is empirically hard to study dispersal patterns and population connectivity of such species, largely due to the adult and larval size, behaviour and habitat complexity (Kozuka, 2008). As a way forward, combining genetic, biological and habitat-related influences (e.g. oceanic currents and tidal fluctuations) can be used to tease apart the complexities of both local and global scale impacts



**FIGURE 2** Results of the Bayesian clustering algorithm STRUCTURE v2.3.4 (Pritchard et al., 2000) for 2–4 genetic groups of the burrowing mud shrimp *Trypaea australiensis* at three sampling sites along the East Coast of New South Wales, Australia between September 2018 and August 2019.



**FIGURE 3** Linear discriminant function 1 versus 2 for the burrowing mud shrimp *Trypaea australiensis* at three sampling locations along the East Coast of New South Wales, Australia between September 2018 and August 2019. Colours represent sampling locations at Port Hacking (light grey), Shoalhaven Heads (dark grey) and Moruya (black).



on marine species management (i.e. “seascape genetics”) (von der Heyden, 2009). The lack of distinct populations within the spatial scale of this study (~250km), which was based on previous research on related species (Kozuka, 2008; McMillen-Jackson & Bert, 2004), suggests that similar studies should encompass the geographic range of the species, and future studies for *T. australiensis* should extend from northern Queensland and Victoria and South Australia. In addition, investigating the impacts of oceanic and tidal currents on larval dispersal and migration would increase understanding of environmental factors that influence larval dispersal and migration of this species. While we recommend further study to shed light on the dynamics of the species as a whole, we have found that *T. australiensis* can be managed as a single stock within a large portion of their range along the NSW coast.

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## CONFLICT OF INTEREST STATEMENT

All authors have no competing interests to declare that are relevant to the content of this article.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study will be made readily available. Fastq files can be accessed through NCBI's Sequence Read Archive (BioProject accession: PRJNA956596; SRA accession numbers SRR24199894–SRR24200052).

## ETHICS STATEMENT

No approval of research ethics was required, as experimental work was conducted with an invertebrate species not regulated by the University of Wollongong ethics committee. However, the authors declare that all necessary approvals for the sampling of specimens have been obtained and conducted under a Fisheries New South Wales permit (permit no. F95/269-8.2), ensuring animal welfare and correct sampling were completed.

## CONSENT TO PARTICIPATE

All authors consent to participate.

## CONSENT TO PUBLICATION

All authors and all institutions that provided funding and to which the authors belong consent to the publication of this study.

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