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Distribution and abundance of toheroa at Oreti Beach, Murihiku/Southland, 2016–17

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Toheroa (*Paphies ventricosa*) is a large species of surf clam that is endemic to New Zealand. Its populations are found in North and South Island regions, where they are most abundant on exposed west coast beaches. This species is of cultural importance and treasured as kai moana, with toheroa populations historically targeted in extensive commercial, recreational and customary fisheries throughout the country. As these populations experienced substantial fishing pressure, marked population declines led to fishery restrictions and closures. In spite of these measures, toheroa populations have shown little recovery to date, and the only take currently permitted is under the customary permit system.

The main southern toheroa populations are found in Murihiku, Southland including Oreti Beach, which supports the largest toheroa population in this region. Toheroa at this beach has been regularly surveyed since 1969, providing information about population trends, with consistent survey methods in recent years (i.e., since 1998) allowing direct comparisons across recent surveys. The current study presents the most recent toheroa assessment at this beach, based on survey data collected in 2016–17. The assessment focused on the population abundance and size structure of toheroa, including population estimates for juveniles (<40 mm shell length) and toheroa ≥40 mm shell length at this beach.

Current abundance estimates for the toheroa population included 2 154 000 (95% CI: 1 602 000–2 706 000) individuals ≥40 mm shell length in 2016–17. Most of the toheroa ≥40 mm were at sizes that exceeded 100 mm shell length, with an estimated 1 279 000 (95% CI: 853 000–1 705 000) individuals in this size class, compared with 875 000 (95% CI: 655 000–1 095 000) medium-sized toheroa (40–99 mm shell length). In addition, the population contained a substantial number of juveniles, with an estimated 8 507 000 (95% CI: 3 082 000–13 932 000) toheroa that were smaller than 40 mm shell length. All of the current estimates reflected increases in the toheroa population, especially in the abundance of juvenile toheroa, which showed an almost four-fold increase from the preceding estimate of 2 052 000 (95% 755 000–3 348 000) juveniles in 2013–14. Since juvenile toheroa were first (systematically) included in the surveys in 1998, their abundance consistently declined across surveys, to the lowest estimate in 2013–14. The current study documents the first increase in the population of juveniles, indicating a strong recruitment event preceding the field survey in 2017.

The spatial distribution of toheroa varied along the beach, and was dependent on the size class. Toheroa ≥40 mm shell length were widely distributed along most parts of Oreti Beach, with particularly high concentrations at the southern end, close to New River Estuary. The southern area was also important for juvenile toheroa, with markedly fewer juveniles occurring in other areas. The significance of the southern end of the beach has been highlighted in previous surveys, and this area continues to be important for the toheroa population. At the same time, there were few toheroa at the northern end, past Waimatuku Stream. Across the beach, toheroa ≥40 mm shell length showed a general preference for the mid- and low-intertidal zones, whereas juveniles were more restricted to high-tide areas.

The population size structure was dominated by the high number of juveniles at Oreti Beach. Length-frequency distribution documented a strong mode of these small individuals, with a considerably smaller mode of large toheroa. At the same time, medium-sized individuals were scarce. The current population size structure is characteristic of the Oreti Beach population and consistent with previous findings.

The findings from the present survey document the persistence of the toheroa population at Oreti Beach, in spite of the low number of juveniles in the preceding survey in 2013–14. Furthermore, the first documented increase in juveniles since 1998 suggests strong recruitment, with potential to augment the existing toheroa population at this site. The southern end of the beach continues to be an important area, including recruiting juveniles and adult toheroa. With only small toheroa populations remaining at other southern sites, Oreti Beach continues to support the main southern population of this species.

1. INTRODUCTION

New Zealand's exposed coastal environments support a number of marine bivalves that are important target species in commercial, customary and recreational fisheries (King & Lake 2013, Hartill et al. 2005). These bivalves include endemic surf clams such as toheroa *Paphies ventricosa* and its congeners tuatua (*Paphies donacina* and *Paphies subtriangulata*), which inhabit the intertidal zone of exposed, open beaches in different parts of the country (Greenway 1969). Toheroa in particular is of cultural significance, and treasured as kai moana.

Toheroa inhabit the sediment of physically-dynamic beaches, where they burrow to 20–30 cm sediment depth. Large, adult toheroa are generally found in the mid- to low-intertidal zone, whereas juveniles settle in the upper region of the surf zone before moving downshore as they increase in size (Redfearn 1974). Toheroa feed on phytoplankton (microalgae) in the water column by extending their siphons into the sediment-water interface during tidal immersion (Morton & Miller 1973).

Southern toheroa have been documented to have two main reproductive periods, with the primary spawning season in spring, and a second spawning event in autumn (Gadomski & Lamare 2015). Their initial growth is considered to be rapid, reaching about 70 mm shell length within the first year, and sexual maturity at 76 mm shell length (Beentjes & Gilbert 2006a, 2006b), although an early study of northern toheroa found that all individuals at 47 mm shell length were mature (Redfearn 1974).

Toheroa has a long history of exploitation, including the development of substantial commercial fisheries in the late 1800s in northern North Island, and also considerable fishing pressure from non-commercial and customary take throughout the country. Prior to exploitation, toheroa was highly abundant in different New Zealand regions, with the main populations in Te Taitokerau/Northland, and smaller populations in other regions such as Kapiti and Horowhenua, and Murihiku/Southland (Oreti Beach and Te Waewae Bay) (Redfearn 1974, Heasman et al. 2012). As fishing impacts led to marked population declines, fishery closures and restrictions were implemented, starting in the 1930s. Nevertheless, toheroa populations continued to decline, in spite of continuing fishing restrictions and subsequent bans. To date, toheroa populations have shown few signs of recovery throughout New Zealand, and the only take currently permitted is under customary management by kaitiaki.

The cultural significance of toheroa and its importance as a fishery species are reflected in the long history of population surveys and monitoring programmes that have been conducted at different North and South Island beaches inhabited by the bivalve (e.g., see overview in Williams et al. 2013a). In Murihiku, Southland, toheroa is specifically mentioned in the Department of Conservation's conservation management strategy, which recognises the significance of local beaches as toheroa habitat, and the threat posed by vehicles driving on beaches (Department of Conservation 2016). This management strategy also highlights the need for collaborations to protect local toheroa populations.

In the southern region, Oreti Beach supports one of the largest toheroa populations in New Zealand, and the main South Island toheroa population (Figure 1). Other southern toheroa sites include Bluecliffs Beach and Orepuki Beach in Te Waewae Bay, but populations at these beaches are small (Berkenbusch et al. 2015). Bluecliffs Beach used to support a large toheroa population, but significant habitat changes have led to a substantial reduction in the distribution and abundance of toheroa in recent times (Beentjes et al. 2006, Beentjes 2010b). These changes have included erosion of the beach, continued receding of the sand dunes, and exposure of stones, leading to the loss of suitable toheroa habitat. Recent survey data revealed the ongoing decline of toheroa at this site, with an estimated 65 000 (95% CI: 0–150 000) toheroa $\geq$40 mm shell length in 2013–14, spread across two disjunct areas, including the western bay (Berkenbusch et al. 2015). Similarly, Orepuki Beach only contains a small toheroa population, which was estimated at 28 000 (95% CI: 10 000–46 000) individuals $\geq$40 mm shell length in 2013–14 (Berkenbusch et al. 2015).

The toheroa population at Oreti Beach has been monitored since 1969, with the most recent survey in 2013–14 (Berkenbusch et al. 2015). This survey showed that the population size of toheroa $\geq$40 mm shell length was relatively stable, but there was a marked decline in the number of juveniles ($<$40 mm shell length); their abundance dropped to a third of the previous estimate in 2009. The low number of juveniles in 2013–14 confirmed a continued decline in this size class since 1998, but the reasons for this decline are unknown.

One of the factors implicated in the decline of juvenile toheroa was the increase in the proportion of gravel at Oreti Beach (Berkenbusch et al. 2015). While previous surveys contained no records of gravel, the latter was present in almost 24% of all sampling points in 2013–14. Statistical modelling indicated a negative association between juvenile toheroa and the presence of gravel, suggesting that this change in habitat may have contributed to the decrease in the number of juveniles.

Other factors that impact toheroa include vehicle traffic and habitat erosion (Williams et al. 2013a). At Oreti Beach, vehicle traffic has been shown to negatively affect toheroa, for example through physical damage to juveniles, and the average annual mortality caused by vehicles was estimated at about 23% of the juvenile population (Moller et al. 2014). At Bluecliffs Beach, loss of habitat through the change from sand to gravel over extensive areas of beach led to a substantial reduction in the distribution and abundance of toheroa (Beentjes & Gilbert 2006a), and the southern end of Oreti Beach has undergone substantial erosion recently (i.e., in 2015, K. Berkenbusch, pers. obs.). This area has consistently supported relatively high concentrations of toheroa in the past, including juveniles that are mainly found in the upper shore region, close to the dunes. Changes in this area may contribute to declines in the juvenile toheroa population.

The present study continues the series of toheroa population surveys at Oreti Beach. Its overall objective was "to determine the distribution of toheroa (*Paphies ventricosa*) beds, and the abundance and size structure of toheroa at Oreti Beach".

2. METHODS

The general sampling methods followed previous toheroa surveys at Oreti Beach commissioned by MPI (e.g., Beentjes 2010a, Berkenbusch et al. 2015). Consistent with these earlier surveys (i.e., since 1998), the sampling was based on a two-phase, stratified random transect sampling design, and conducted during summer. Oreti Beach was divided alongshore into sections, or strata, with a number of transects sampled within each stratum. The overall goal of the survey was to estimate toheroa abundance within the sampled areas, with a coefficient of variation of less than 20% for the total number of toheroa $\geq$40 mm shell length.

The stratification was based on previous survey data, resulting in seven strata along Oreti Beach that were consistent with the preceding survey in 2013–14 (Figure 2). This earlier survey determined strata boundaries based on toheroa population information, and included the merging of previous strata 3 and 4 (now stratum 3), and strata 5 and 6 (now stratum 4). In addition, the 2013–14 survey extended the southern boundary of the sampling region to include an area close to New River Estuary as an additional stratum (now stratum 1), including an area known as "the reserve". The southern boundary of stratum 1 was defined by the edge of the broad beach. At the northwestern end, the sampling region extended beyond the mouth of Waimatuku Stream, to an area where the beach narrowed. The main entrance to the beach was at the boundary of strata 4 and 5, about 7.8 km north of New River Estuary.

Within each stratum, the starting positions of the transects were randomly allocated, with the restriction that the start positions were a minimum of 20 m apart. The start positions were assigned along a line that traced the toe of the dune (using satellite imagery in a geographic information system). The initial phase-1 transects and potential phase-2 transects were allocated before the field survey began. A minimum of four transects was allocated to each stratum, and remaining phase-1 transects were allocated to sequentially maximise the area-mean-squared, based on previous toheroa survey data. Phase-2 transects were allocated following phase-1 sampling, based on data from the first phase.

The transect allocation resulted in a total of 33 transects for phase 1, and seven transects were retained for allocation in phase 2 (Figure 2). The phase-1 transects included four transects each in strata 1, 3, and 4, five transects each in strata 2, 5, and 6, and six transects in stratum 7. Two of the phase-1 transects from

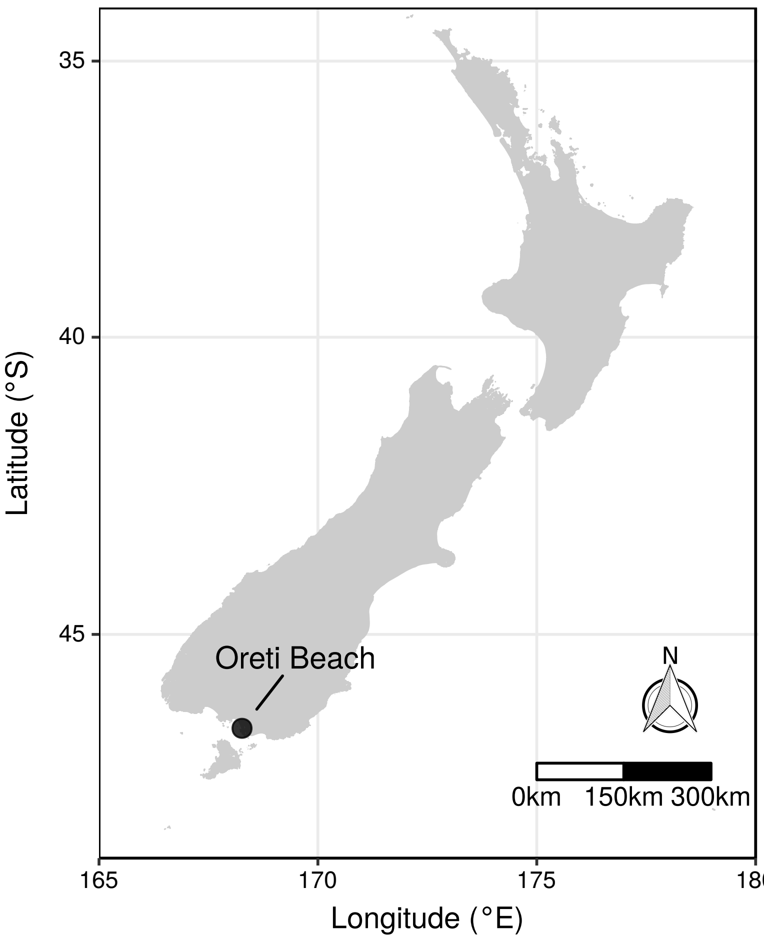


Figure 1: Location of the southern toheroa population at Oreti Beach in Murihiku/Southland that was surveyed in 2016–17.

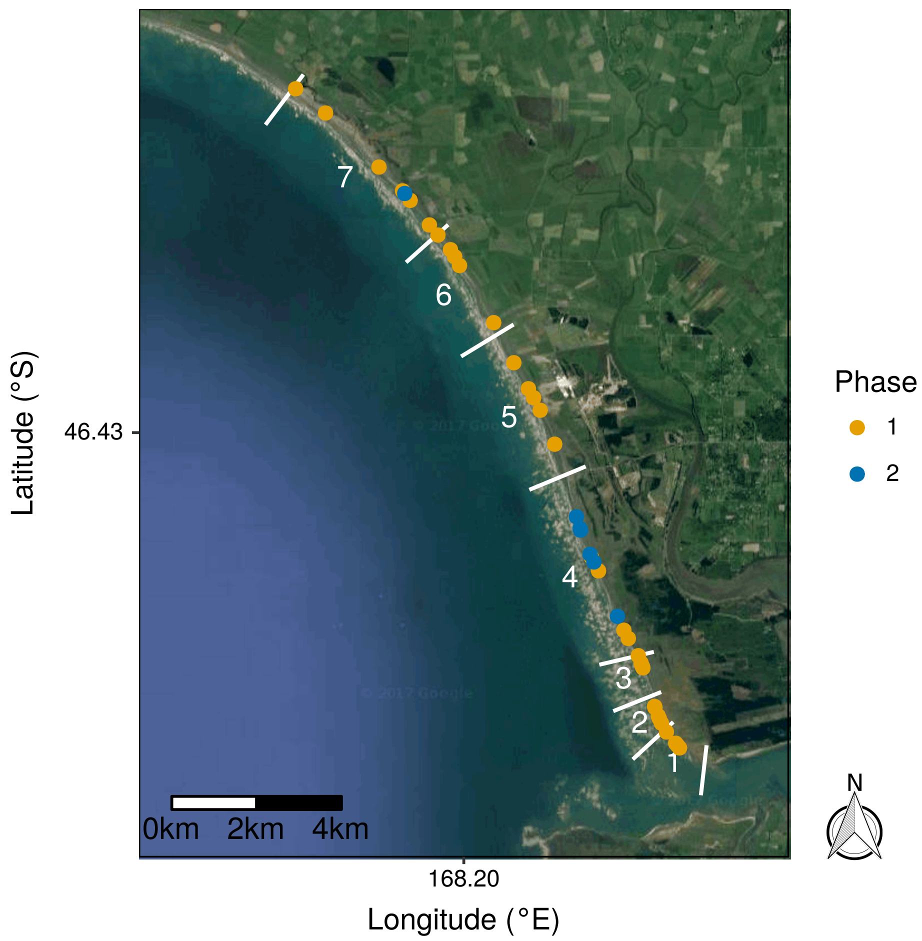


Figure 2: Sampling strata at Oreti Beach used for surveying toheroa in 2016–17, including starting points for phase 1 and 2 transects. The main entrance to the beach is at the boundary of strata 4 and 5.

each stratum were randomly allocated to be sieved on 5-mm mesh to determine the number of juvenile toheroa, i.e., individuals larger than 5 mm shell length and smaller than 40 mm shell length. Following the phase-1 sampling, seven transects were sampled in phase 2, including six transects in stratum 4, and one transect in stratum 7.

The field data were used to estimate toheroa abundance, applying the same estimation methods used previously (e.g., Beentjes & Gilbert 2006b, Beentjes 2010a, Berkenbusch et al. 2015). The number of toheroa within each size class was estimated by scaling up the counts in each quadrat to account for the fraction of each transect that was sampled, and then to account for the fraction of the length of each stratum that was covered by the width of the transects. The uncertainty was calculated using an analytical expression, appropriate for stratified random sampling (Cochran 1977).

Formally, if a quadrat, q, had a number of toheroa, n_{qc}, in size class, c, then the total estimated number of toheroa, $\hat{n}_{tc}$, in that size class in transect t, was estimated as:

$$\hat{n}_{tc} = \frac{1}{f} \sum_{q \in t} n_{qc}, \tag{1}$$

where f was the fraction of the transect that was sampled (the ratio of the quadrat size to the distance between quadrats), and the sum was over all the quadrats in the transect. The estimated total number of toheroa, $\hat{N}_c$, in size class c at Oreti Beach was then:

$$\hat{N}_c = \sum_s \text{Mean}_s(\hat{n}_{tc}) \frac{l_s}{w}, \tag{2}$$

where l_s was the length (in metres) of stratum s, w was the width of the transects, and the mean, Mean_s was calculated over all transects in stratum s. Abundance was separately estimated within each stratum, and then summed over all strata at Oreti Beach. The abundance estimates distinguished different size classes, including toheroa <40 mm shell length (juveniles), and individuals at ≥40 mm, 40–99 mm, ≥80 mm, and ≥100 mm shell lengths. These size classes were chosen for comparison with previous assessments.

On two phase-1 transects in each stratum, all quadrats were sieved to ascertain the number of toheroa that were larger than 5 mm shell length. This sampling approach was taken to reliably sample toheroa <40 mm shell length (juveniles). For the estimation of the number of juveniles, only data from these sieved transects were included. The number of juveniles was estimated considering the whole beach as a single stratum for the purpose of this estimation. The total number of toheroa was then calculated by combining the separate estimates of toheroa that were <40 mm and toheroa ≥40 mm shell length.

For the estimation, it was assumed that the transects crossed through the zone of the beach where toheroa are found (so that there were no toheroa beyond the end of the transects). There was no extrapolation in the counts beyond the length of the transects, or beyond the defined strata, so the estimates are restricted to this sampling region. The length of the strata was calculated at the toe of the dune, and it is possible that there curvature of the beach leads to some error in scaling up from the transects to the whole strata. Following previous studies (e.g., Beentjes 2010a, Berkenbusch et al. 2015), this effect was considered to be inconsequential.

The variance of the estimate was calculated as follows (Cochran 1977):

$$\hat{V}_c = \sum_s \text{Var}_s(\hat{n}_{tc}) \frac{1}{t_s} \left(\frac{l_s}{w}\right)^2, \tag{3}$$

where t_s was the number of transects in stratum s, and the variance, Var_s was calculated over all the transects in stratum s. The uncertainty in the estimates was expressed as the coefficient of variation, $\text{CV}_c = \sqrt{V_c}/N_c$. A 95% confidence interval for the mean abundance estimates was calculated as $\hat{N}_c(1 \pm 1.96\text{CV}_c)$, by assuming that the error in the mean was normally distributed. In presentation of the confidence intervals for strata with uncertain estimates, the lower confidence interval was truncated at zero if it would otherwise have been negative.

To allocate the transects to the strata, the area-mean-squared approximation was used (Francis 1984), with the gain in adding a transect to a stratum being:

$$\text{AM}^2 = \text{Mean}_s(\hat{n}_t)^2 \frac{l_s^2}{t_s(t_s+1)}, \tag{4}$$

where $\hat{n}_t$ was here the number of toheroa ≥40 mm shell length.

2.1 Sampling methods

The field sampling of toheroa was conducted at low tide over consecutive days between 9 and 17 January 2017. The sampling dates were chosen to coincide with a period of low tide that had the lowest tidal height over that period, generally <0.5 m above chart datum.

The field sampling started by locating the starting position of each transect at the toe of the dune using global positioning system (GPS) units (see Appendix A for transect locations). Each transect extended from the toe of the dune, through the GPS position that marked the transect, across the beach to the low water mark. The first quadrat of each transect was 5 metres from the toe of the dune. Subsequent quadrats were evenly spaced at 5-m intervals along the transect, and sampled for toheroa. The location of each sampling point was recorded using GPS units.

Sampling quadrats were 0.5 m by 0.5 m in size, and excavated to 30 cm depth (as in 2013–14, see Berkenbusch et al. 2015). Sediment from each quadrat was carefully sorted at the sediment surface to detect any toheroa (i.e., $\geq$40 mm shell length). All toheroa in the quadrats were counted and their shell length was measured (with the measurement rounded down to the nearest whole millimetre), before returning them to the sediment. When individuals were damaged during excavation, their shell length was estimated.

On transects that were sieved to assess the abundance of juvenile toheroa, the sediment from each quadrat was directly transferred into box sieves and sieved on 5-mm mesh. All toheroa retained on the mesh were counted and measured in the field before they were returned to the sediment.

In addition, at each sampling point, the sediment in the quadrat was qualitatively assessed for the presence of gravel (i.e, sediment grain size $>$2 mm). No attempt was made to quantify the amount of gravel in each quadrat.

3. RESULTS

3.1 Sampling

The current survey at Oreti Beach included a total of 40 transects, with 33 transects in the first phase and seven transects in the second phase (Table 1). The lengths of strata varied from 869 m (stratum 2) to 4881 m (stratum 7). The widths of the beach (or strata) determined the lengths of transects in each stratum. The average transect length varied from 149 m in stratum 1 to 231 m in stratum 3.

Each stratum included two transects that were sieved to determine the number of juvenile toheroa (defined as larger than 5 mm and smaller than 40 mm shell length). Across the 14 transects, a total of 506 quadrats were sieved, sampling a total of 311 juvenile toheroa.

Most strata included quadrats that contained gravel (qualitatively assessed during sampling; see Appendix A). There was a relatively high proportion (over 30%) of quadrats with gravel in strata 1, 6, and 7, with the highest percentage in stratum 7 (51%). There were fewer quadrats with gravel in strata 2 and 5 (16% and 5%, respectively). Strata 3 and 4 had no gravel recorded.

Table 1: Strata used for estimating toheroa abundance at Oreti Beach in 2016–17. Included are the stratum length (along the beach), the width of the beach (the mean length of the transects), the number of transects per phase and in total, the number of quadrats sampled, and the percentage of quadrats with gravel in each stratum.

Stratum	Length (m)	Width (m)	Transects			Quadrats	Gravel (%)
			Phase 1	Phase 2	Total		
1	1258	149	4	0	4	123	33
2	869	180	5	0	5	185	16
3	1008	231	4	0	4	189	0
4	4634	168	4	6	10	345	0
5	3717	164	5	0	5	169	5
6	2781	148	5	0	5	153	48
7	4881	184	6	1	7	265	51

Table 2: Estimated abundance and density of toheroa in each stratum with shell lengths ≥40 mm at Oreti Beach in 2016–17. Included are the number of toheroa counted in the sampled quadrats (N), estimated mean abundance (number of toheroa) with 95% confidence interval (CI) and coefficient of variation (CV), and the estimated mean density (number of toheroa per linear metre of beach) with 95% CI.

Stratum	N	Abundance			Density	
		Mean	95% CI	CV (%)	Mean	95% CI
1	25	157 000	86 000–228 000	23.0	125	69–181
2	74	257 000	141 000–373 000	23.0	296	163–429
3	35	176 000	136 000–217 000	11.8	175	135–215
4	43	399 000	180 000–617 000	28.0	86	39–133
5	24	357 000	240 000–473 000	16.7	96	65–127
6	30	334 000	0–707 000	57.0	120	0–254
7	34	474 000	184 000–765 000	31.3	97	38–157

3.2 Toheroa abundance estimates

Toheroa were present in all strata, with the highest estimated mean number of toheroa ≥40 mm shell length in stratum 7, at the northwestern end of the survey area. There were an estimated 474 000 (95% CI: 184 000–765 000) toheroa ≥40 mm shell length in this stratum. Numbers of toheroa ≥40 mm shell length were also relatively high in other northwestern strata, including strata 4 to 6, but the abundance estimate in the latter stratum had high uncertainty (i.e., CV; 57.0%).

In comparison to the abundance estimates across individual strata, densities of toheroa ≥40 mm shell length were highest in southern strata 2 and 3, close to New River Estuary. In these strata, estimated densities were 296 and 175 individuals in this size class per linear metre of beach, respectively (Table 2). The lowest estimated mean densities were in strata 4 and 5 (on either side of the main entrance of the beach) and in stratum 7, ranging between 86 and 97 individuals ≥40 mm shell length per linear metre of beach.

Based on the survey data, the total number of toheroa ≥40 mm shell length at Oreti Beach was estimated at 2 154 000 (95% CI: 1 602 000–2 706 000) individuals in 2016–17 (Table 3). Over half of these toheroa were individuals that were at least 100 mm shell length, with 1 279 000 (95% CI: 853 000–1 705 000) toheroa in this size class. The uncertainty of these estimates was relatively low, all of the estimates of toheroa size classes ≥40 mm shell length had a CV of less than 20%. For this part of the toheroa population, including all individuals with shell lengths ≥40 mm, the CV was 13.1%.

In addition to large individuals, there was a substantial number of juvenile toheroa (<40 mm shell length) at Oreti Beach, with an estimated 8 507 000 (95% CI: 3 082 000–13 932 000) toheroa in this size class in 2016–17 (Table 3). This estimate was about four times the abundance of all toheroa ≥40 mm shell length, but the uncertainty of the estimate for the juvenile size class was higher than for the larger size classes, with a CV of 32.5%. The estimated mean density of juveniles was 444 (95% CI: 161–728) toheroa per linear metre of beach.

Table 3: Estimated number of toheroa at Oreti Beach surveyed in 2016–17. Included are the mean estimate, 95% confidence interval (CI), and the coefficient of variation (CV) for each of the different size classes. The size class of toheroa ≥80 mm shell length was included to allow comparisons with previous estimates.

Beach	Size	Mean	95% CI	CV (%)
Oreti	< 40 mm	8 507 000	3 082 000–13 932 000	32.5
	≥ 40 mm	2 154 000	1 602 000–2 706 000	13.1
	40–99 mm	875 000	655 000–1 095 000	12.9
	≥ 80 mm	1 573 000	1 096 000–2 050 000	15.5
	≥ 100 mm	1 279 000	853 000–1 705 000	17.0
	All	10 661 000	5 208 000–16 114 000	26.1

3.3 Spatial distribution of toheroa

Considering the spatial distribution of toheroa across the beach, there were distinct patterns across the intertidal area with marked differences between toheroa ≥40 mm shell length and juveniles (Figure 3). Toheroa ≥40 mm shell length were predominantly in the mid- to low-intertidal zone, with highest densities at about 100 to 200 m distance from the toe of the dune. There were few individuals in this size class in the upper intertidal, nor close to the low tide mark. In contrast, juvenile toheroa were more broadly distributed across the beach, and their highest densities were in the upper intertidal area. Compared with toheroa ≥40 mm shell length, juvenile densities were relatively high at the toe of the dune, and increased with distance from the dune to a distinct peak at about 75 m distance. Their densities then declined with further distance from the dune, but showed another increase at about 150 to 200 m distance. Juveniles were present across the entire intertidal area of the beach, except at the low tide mark.

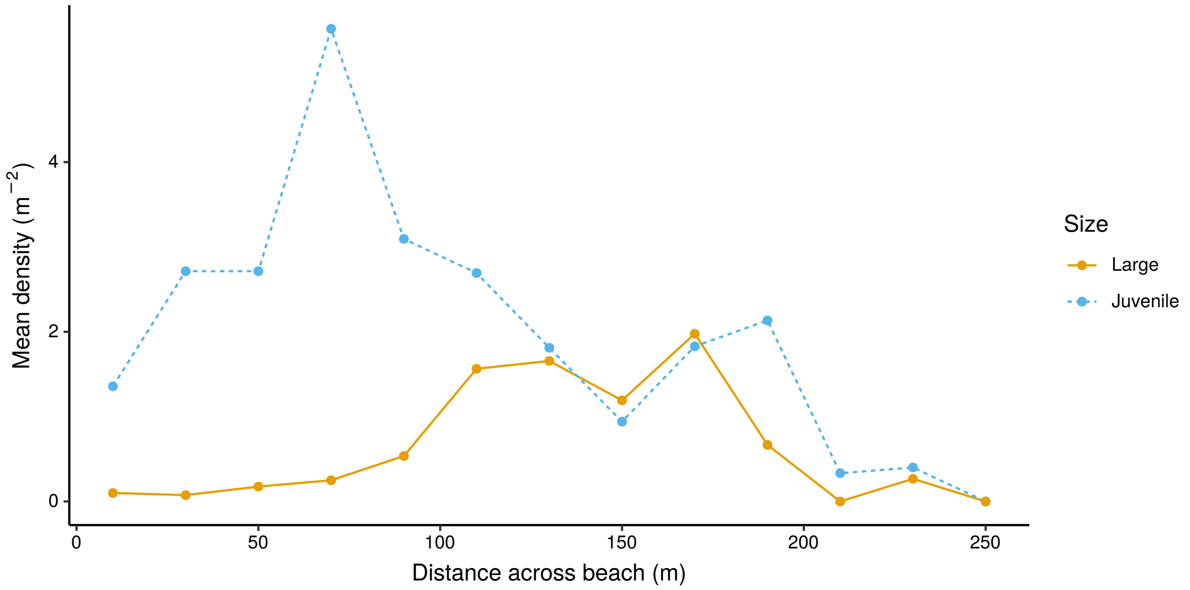
The spatial distribution of toheroa along the beach also highlighted some differences in the areas occupied by toheroa ≥40 mm shell length and juvenile toheroa (Figure 4). Both size groups were prevalent at the southern end of Oreti Beach, in the area close to New River Estuary. Within this area, individuals ≥40 mm shell length were particularly concentrated within one to two kilometres from the estuary entrance, where they were present at comparatively high densities across the entire beach. In other areas along the beach, high-density patches of these individuals were more confined across the beach, generally in the mid-intertidal, such as at distances of about 8.5 km and also 14–15 km from the estuary. There were few toheroa ≥40 mm shell length at the northern end of the beach, or immediately south of the main road entrance at about 7 km from the estuary mouth.

The highest densities of juveniles were also at the southern part of the beach, especially at about 3 km from the estuary mouth. In the southern area, juveniles occurred across the intertidal zone, whereas they were considerably more restricted in other areas, generally to the upper intertidal. Both their distribution and their densities were restricted in areas other than at the southern end, where they were consistently present in transects. Similar to toheroa ≥40 mm shell length, there were only few juveniles at the northern end.

3.4 Toheroa size distributions

Length-frequency distributions of the toheroa population confirmed the dominance of juveniles at Oreti Beach (Figure 5). Although the population was bimodal, juveniles represented a considerably stronger cohort than individuals ≥40 mm shell length. The former size class was determined by toheroa at 5 to 30 mm shell length, with the strongest size mode at 5 to 10 mm shell length. In comparison, larger individuals were primarily >100 mm shell length, and had little influence on the population size structure. At the same time, medium-sized toheroa were scarce, with few individuals at sizes between 50 and 99 mm shell length.

(a) Toheroa density



(b) Number of quadrats

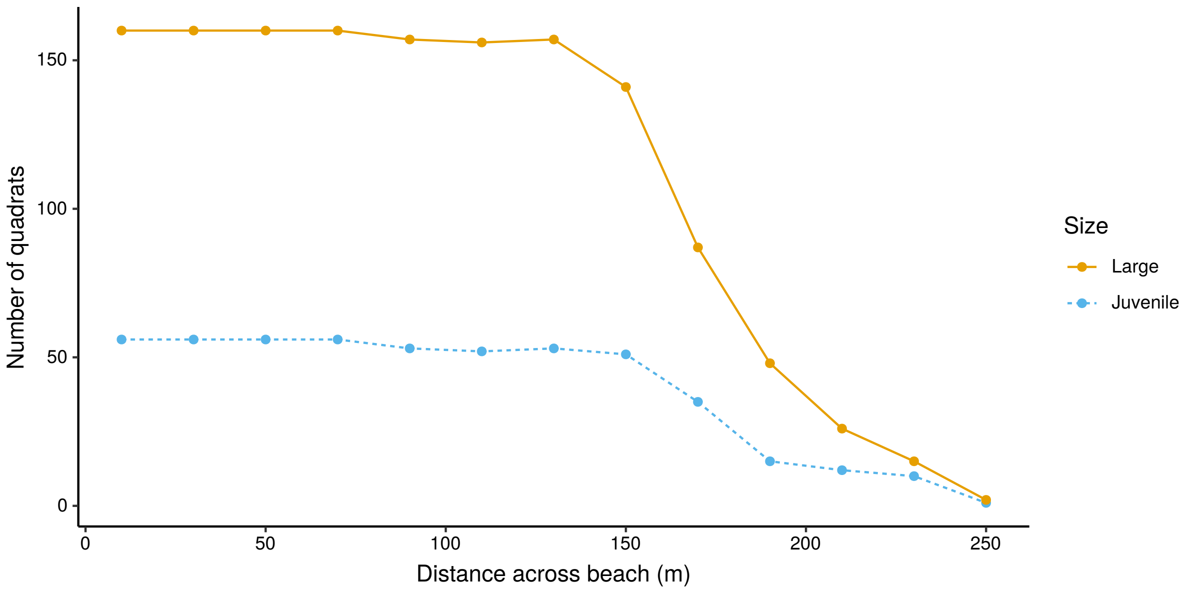
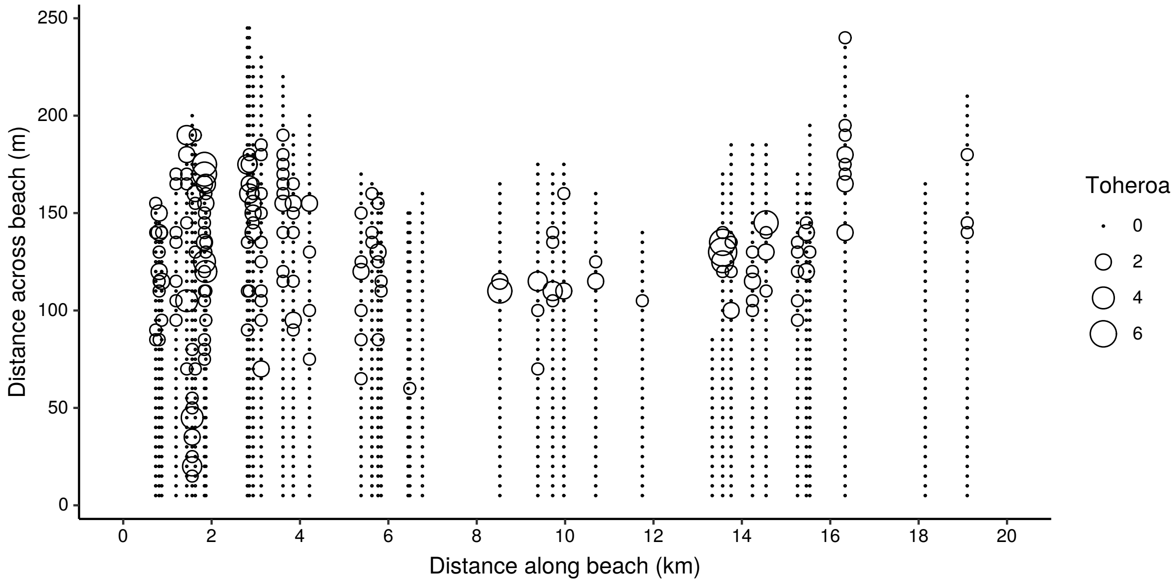


Figure 3: Mean density of toheroa (m^{-2}) for toheroa ≥40 mm shell length and juveniles (<40 mm shell length) in 2016–17, by distance across the beach (from the toe of the dune). Presented are (a) the mean density (averaged in 20-m bands), and (b) the number of quadrats sampled. Data for toheroa ≥40 mm shell length were based on all sampled quadrats, whereas data for juvenile toheroa were based on sieved transects only.

(a) Large toheroa



(b) Juvenile toheroa

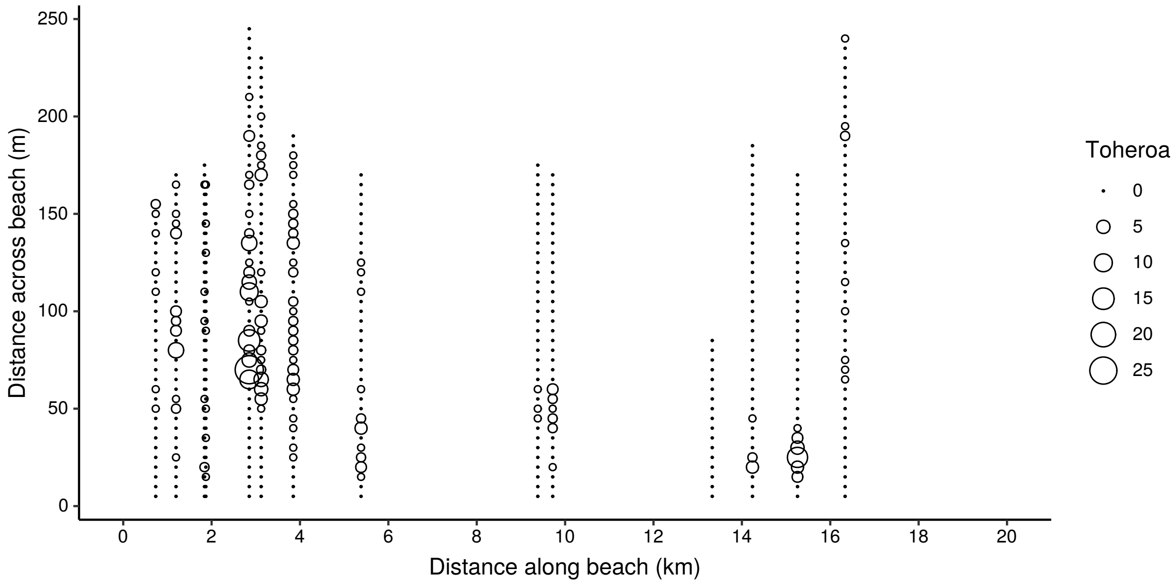


Figure 4: Distribution of toheroa at Oreti Beach, by distance along the beach (from New River Estuary) and distance across the beach (from the toe of the dune). Dots indicate the position of sampled quadrats, and circle sizes correspond with the number of toheroa sampled. Large toheroa were $\geq$40 mm shell length and juvenile toheroa were $<$40 mm shell length. Data for large toheroa were based on all sampled quadrats, while data for juvenile toheroa were based on sieved transects only. (The main entrance of the beach is about 7.5 km from the estuary.)

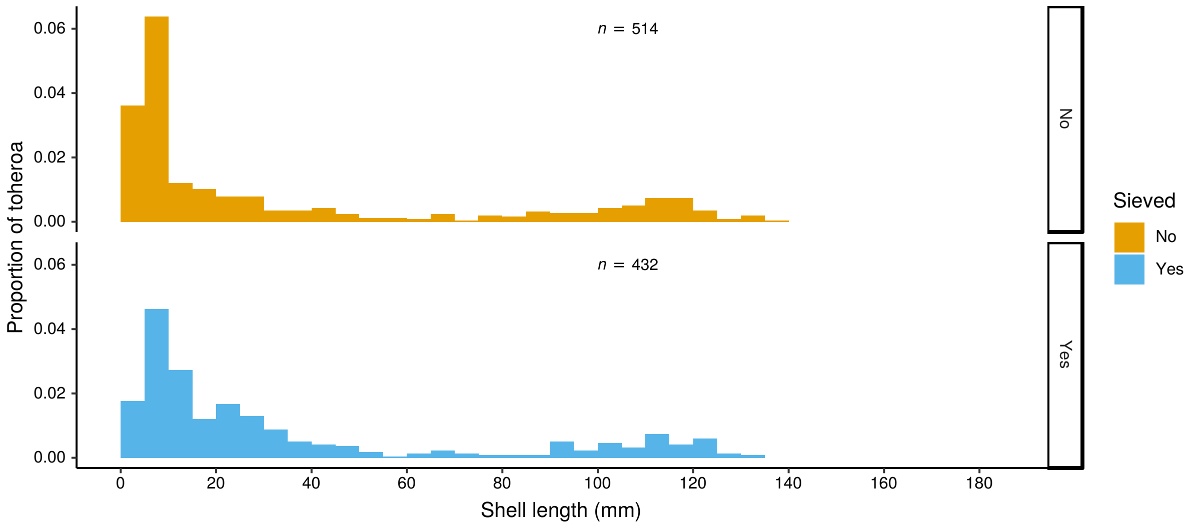


Figure 5: Size-frequency distributions of toheroa at Oreti Beach in 2016–17. Data were from non-sieved and sieved transects (sample sizes indicate the number of toheroa measured).

Comparing shell length data from the sieved and non-sieved transects revealed a similar population size structure, although there fewer toheroa at sizes between 15 and 35 mm shell length in the non-sieved quadrats.

4. DISCUSSION

The current study presents the most recent population estimates of toheroa at Oreti Beach, updating population information from the preceding survey in 2013–14 (Berkenbusch et al. 2015). The field sampling focused on the same area as the 2013–14 survey, including the southern reserve, allowing direct comparisons between the two surveys. Earlier toheroa population data are also available from other previous surveys at this beach, as regular population assessments have been carried out since 1969. Even though the survey methods have varied over time, the latter have been relatively consistent since 1998, including stratified random transect sampling and the systematic inclusion of juveniles in the survey (by sieving a subset of transects) (Beentjes 2010a). Nevertheless, not all recent surveys have included the southern reserve (Millar & Olsen 1995). One change in the two most recent surveys was the reduction of the sampling quadrat, halving the surface area to 0.5 m by 0.5 m. This quadrat size has also been used in northern toheroa surveys (Williams et al. 2013b), and did not affect the estimates here, as indicated by CV values well below 20%.

Based on the 2016–17 field survey, the current population estimate for toheroa ≥40 mm shell length at Oreti Beach was 2 154 000 (95% CI: 1 602 000–2 706 000) individuals. This estimate was a substantial increase from the preceding estimate of 1 395 000 (95% CI: 951 000–1 840 000) toheroa ≥40 mm shell length in 2013–14. Similar to the previous survey, most of the individuals in this size class were longer than 100 mm shell length, with an estimated 1 279 000 (95% CI: 853 000–1 705 000) toheroa at these sizes in 2016–17. Their numbers showed a small recent increase compared with their estimate in 2013–14. Medium-sized toheroa were less abundant than the largest individuals, with an estimated 875 000 (95% CI: 655 000–1 095 000) toheroa at shell lengths between 40 and 99 mm. Although they made up a smaller proportion of the population, medium-sized individuals showed a marked increase from their previous abundance estimate of 390 000 (95% CI: 228 000–552 000) individuals in 2013–14. For juvenile toheroa (<40 mm shell length), the 2017–18 abundance estimate indicated a four-fold increase in their population size, from 2 052 000 (95% c.i.: 755 000–3 348 000) individuals in 2013–14 to 8 507 000 (95% CI: 3 082 000–13 932 000) juveniles in the current survey.

Overall, the size structure of the current toheroa population was consistent with previous information from Oreti Beach (e.g., Beentjes 2010a). Except for the preceding assessment, the population at this beach has been typically bimodal, with a strong mode of juveniles, a smaller mode of toheroa in the largest size class (i.e., toheroa ≥100 mm shell length), and few medium-sized toheroa between these two modes. Beentjes & Gilbert (2006b) attributed this population structure and the scarcity of medium-sized toheroa to high mortality of juveniles and rapid growth of the few remaining juveniles to larger size classes. They considered that the latter toheroa constituted several cohorts, ranging in age from five to 20 years (considered to be the maximum lifespan of toheroa; Cassie 1955). These large toheroa are characterised by slow growth and low mortality, leading to the aggregation of different cohorts at the maximum size of this species.

Throughout the survey series, there have been some fluctuations in the population of toheroa ≥80 mm shell length, especially in the early part of the data series (Figure 6). This size class was highly abundant in the 1970s and 1980s before numbers declined and remained low for a considerable period of time. The lowest abundance estimates of individuals ≥80 mm shell length were in 2002 and 2005, and there have been notable increases in their abundance since then. The 2016–17 estimate continued this increase, suggesting that the population of toheroa ≥80 mm shell length is persisting at Oreti Beach, and slowly increasing.

For juvenile toheroa, the current population size is the first documented increase in their abundance since this size class was first systematically included in the surveys in 1998 (Figure 7). Although juveniles have been a significant part of the Oreti Beach population, their overall abundance has continuously declined since 1998. Their initially high abundance of 15 829 785 (95% c.i.: 11 161 065–20 498 505) juveniles in that year decreased to about 10 million individuals in 2002, to the lowest estimate in 2013–14. The recent increase in juveniles indicates a strong recruitment event preceding the current survey, with large numbers of toheroa larvae (spat) settling and recruiting to the benthic population, resulting in the high number of 0+ year individuals.

Toheroa populations are renowned for considerable fluctuations in population dynamics, including variable recruitment and high post-recruitment mortality (Redfearn 1974, Morrison & Parkinson 2001). For this reason, strong recruitment episodes may not necessarily augment adult populations, and it is uncertain what proportion of the strong juvenile size class will subsequently contribute adults. Nevertheless, the increase in medium-sized individuals suggests that a number of recruits settling between the two most recent surveys succeeded to grow to larger sizes, subsequently contributing medium-sized toheroa to the population.

For the spatial distribution of the toheroa population, the southern end of Oreti Beach continues to be significant. Both juveniles and toheroa ≥40 mm shell length have consistently occupied this area at comparatively high densities, including in 2016–17. Erosion in this area has resulted in a narrowing of the intertidal zone, which was evident in the reduced widths of strata 1 and 2 in the current study. For example, the width of stratum 1 decreased from 229 m in 2013–14 to 149 m in 2016–17. Although some of this variation may be owing to differences in tidal level and small-scale changes at the beach, the narrowing of these strata provides some indication of habitat changes in the southern area. The latter was reflected in changes in the distribution of toheroa ≥40 mm shell length in the recent survey, as these individuals were less confined across the intertidal zone, but extended their distribution into the upper intertidal area compared with the previous survey.

A recent review examined factors that may affect toheroa populations in New Zealand, including sources of mortality and potential impacts on recruitment, such as food availability, climate and weather, vehicle traffic, and land use change (Williams et al. 2013a). While toheroa populations are influenced by natural processes, the review suggested that human impacts may reduce their resilience and limit their ability to recover from mortality events or low recruitment.

In view of multiple threats facing toheroa populations throughout New Zealand, the increases in numbers documented in the current survey indicate that the toheroa population at Oreti Beach is persisting. This beach currently supports one of the main toheroa populations in New Zealand, and the only substantial South Island population of this species.

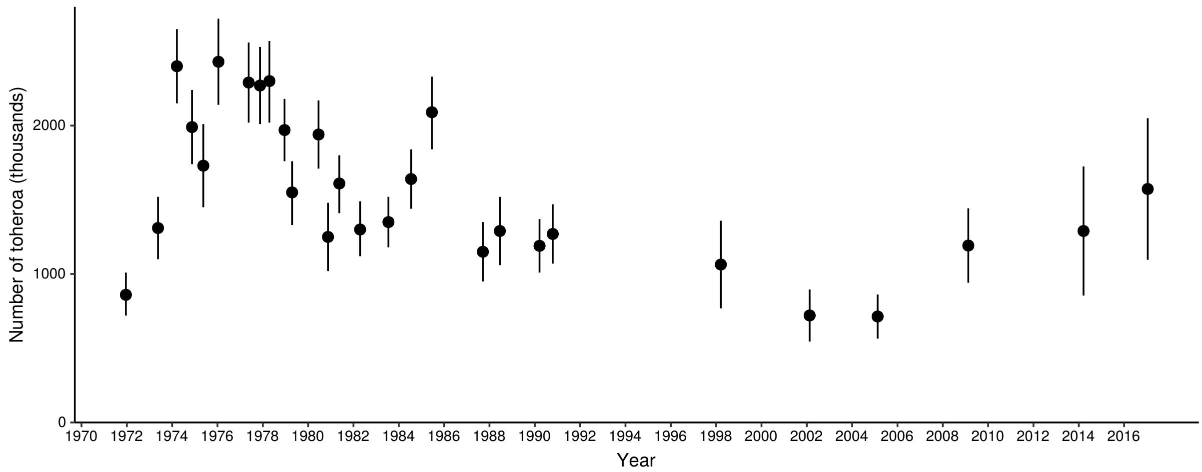


Figure 6: Time-series of the number of toheroa $\geq$80 mm shell length at Oreti Beach. Previous data include estimates from surveys before 1992 (Millar & Olsen 1995) and between 1998 and 2009 (Carbines & Breen 1999, Beentjes et al. 2003, Beentjes & Gilbert 2006b, Beentjes 2010a). The latter surveys did not include the reserve area (stratum 1 in the 2013–14 and 2016–17 surveys). Data from a survey in 1996 (Carbines 1997) were omitted, as the survey transects were truncated and did not cover the entire tidal range of toheroa. Uncertainties in the 1998 survey were not available from the original report (Carbines & Breen 1999), and were constructed using the same coefficient of variation as the estimate of the number of toheroa over 100 mm shell length.

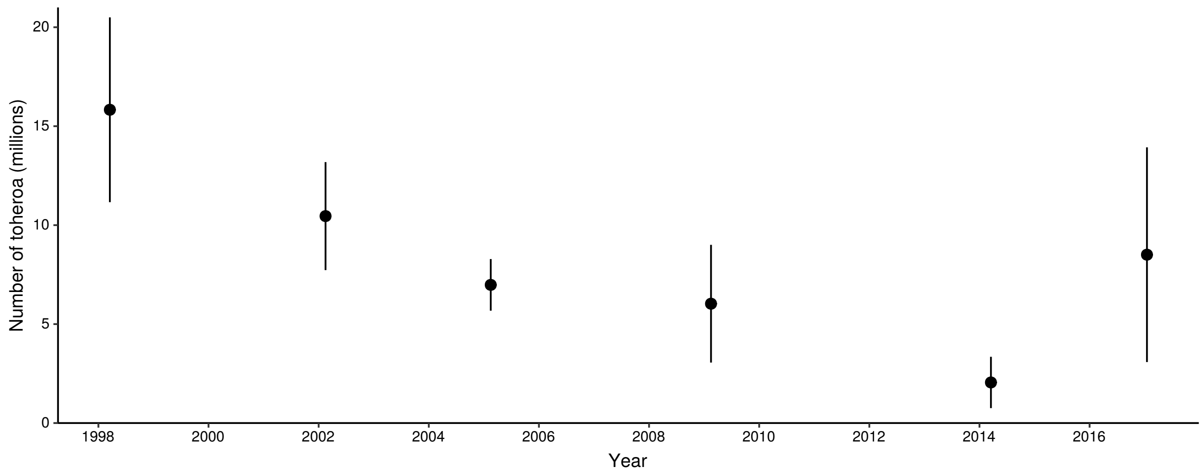


Figure 7: Time-series of juvenile toheroa ($<$40 mm shell length) at Oreti Beach. Previous data include estimates from surveys in 1998 (Carbines & Breen 1999), 2002 (Beentjes et al. 2003), 2005 (Beentjes & Gilbert 2006b), 2009 (Beentjes 2010a), and 2014 (Berkenbusch et al. 2015).

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APPENDIX A: Transect information

Table A-1: Sampling information of the 2016–17 toheroa survey at Oreti Beach. Presented are the stratum and transect numbers, whether transects included sieved quadrats, the percentage of quadrats that contained gravel, and the transect starting points at the toe of the dune (in decimal degrees, World Geodetic System 1984).

Stratum	Phase	Transect	Sieved	Gravel (%)	Latitude	Longitude
1	1	1	Yes	65	-46.4969	168.2665
1	1	2	No	0	-46.4964	168.2658
1	1	3	No	0	-46.4959	168.2653
1	1	4	Yes	62	-46.4935	168.2624
2	1	1	No	21	-46.4917	168.2609
2	1	2	No	0	-46.4907	168.2603
2	1	3	No	0	-46.4901	168.2599
2	1	4	Yes	14	-46.4884	168.2589
2	1	5	Yes	47	-46.4881	168.2588
3	1	1	No	0	-46.4799	168.2552
3	1	2	Yes	0	-46.4796	168.2550
3	1	3	No	0	-46.4789	168.2546
3	1	4	Yes	0	-46.4774	168.2538
4	1	1	No	0	-46.4737	168.2507
4	1	2	Yes	0	-46.4719	168.2493
4	1	3	Yes	0	-46.4593	168.2415
4	1	4	No	0	-46.4564	168.2393
5	1	1	No	0	-46.4325	168.2280
5	1	2	Yes	14	-46.4252	168.2235
5	1	3	Yes	9	-46.4226	168.2215
5	1	4	No	0	-46.4207	168.2199
5	1	5	No	0	-46.4151	168.2154
6	1	1	No	0	-46.4066	168.2092
6	1	2	Yes	100	-46.3945	168.1987
6	1	3	No	91	-46.3926	168.1972
6	1	4	No	0	-46.3911	168.1959
6	1	5	Yes	68	-46.3880	168.1920
7	1	1	No	0	-46.3859	168.1894
7	1	2	Yes	65	-46.3807	168.1835
7	1	3	No	0	-46.3786	168.1811
7	1	4	Yes	44	-46.3736	168.1738
7	1	5	No	15	-46.3621	168.1574
7	1	6	No	43	-46.3569	168.1482
4	2	1	No	0	-46.4690	168.2474
4	2	4	No	0	-46.4575	168.2401
4	2	5	No	0	-46.4558	168.2389
4	2	6	No	0	-46.4507	168.2360
4	2	7	No	0	-46.4504	168.2358
4	2	8	No	0	-46.4479	168.2347
7	2	3	No	100	-46.3792	168.1818