

Comparative study of the Chatham Islands Odonata: Morphological variability, behaviour and demography of the endemic

***Xanthocnemis tuanuii* Rowe, 1987**

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Abstract

Faunistic investigations on adult insects and molecular research on larvae have identified the existence of at least four species of Odonata on the Chatham Islands. The species resemble their New Zealand counterparts, although there are morphological deviations from the typical diagnostic features. Molecular evidence is not concordant with earlier morphological results as far as the genus *Xanthocnemis* is concerned. Genetic data suggest there are two species on the island while morphological investigations revealed just one. This topic needs further clarification and is given special attention in the present study. The main aim of the present study is to establish the taxonomic position of Chatham Island *Xanthocnemis* species and its relation to New Zealand main island fauna. It also provides some data on the biology of the local species and estimates of key demographic parameters (i.e., survival and abundance). The results show that Chatham Islands inhabitants are close morphologically to their New Zealand main island counterparts. Between-island differences in wing area and abdomen-to-body length ratio were found, but were largely attributable to the harsh environment on the Chatham Islands and its influence on body size. Chatham *Xanthocnemis* exhibited low survival rates and a great diversity



of female colour morphs and certain behavioural traits (like underwater oviposition), which are suspected to be due to a composite influence of low summer temperatures, constant winds, and low pH. Ultimately, the taxonomic status of the Chatham Island *Xanthocnemis* species needs further confirmation based on molecular analysis of adults.

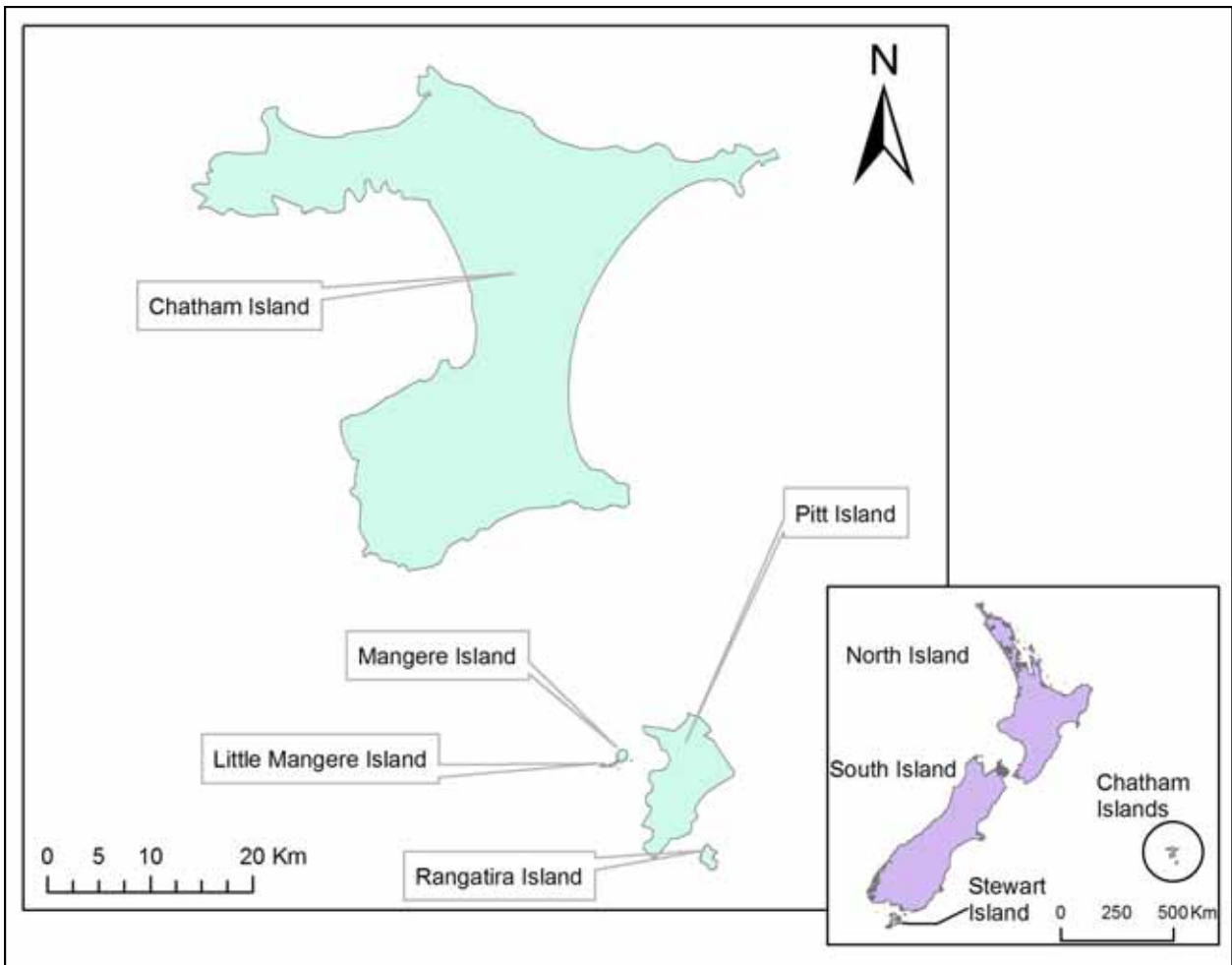


Figure 1. Situation of the Chatham Islands group relative to the New Zealand main islands (North, South and Stewart).

Introduction

The Chatham Islands are situated about 850 km east of the New Zealand main islands (named as the North, South and Stewart) (fig. 1). They consist of five islands and several small islets with Chatham Island (total of 929 km²) being the largest. They have a relatively young geological age as the recent estimations are for 1.8-2.4 million years (Campbell 1998). Various floristic and faunistic studies give evidence



that the young biota has a close relation to New Zealand main islands (reviewed in Goldberg et al. 2008) or even to the Mediterranean (Heenan et al. 2010). Endemism is confined to species level only, but is well demonstrated in some terrestrial groups, such as cave weta *Talitropsis* spp., even within the islands in the archipelago (Trewick 2000). These data suggest that rapid speciation could occur even in a small, young landscape (Goldberg et al. 2008).

While the island terrestrial fauna is well isolated and has a good prerequisite for evolving various lineages, a curious feature of the Chatham Islands is the level of endemism among air-borne insects and birds. Chatham Island taiko (*Pterodroma magentae* (Giglioli & Salvadori, 1869)) and Chatham Island oystercatcher (*Haematopus chathamensis* Turbott 1990) are, perhaps, the most striking examples. This endemism of potentially highly mobile species is a phenomenon that deserves special attention because it may help to elucidate evolutionary patterns of the diversification of life.

Chatham Islands Odonata species closely resemble the New Zealand main islands species. Early investigations assigned specimens to taxa already described from the main islands. Hutton (1898) was the first to give information about Chatham Islands' Odonata. Three species *Xanthocnemis sobrina* (McLachlan, 1873), *Austrolestes colenisonis* (White, 1846) and *Procordulia smithii* (White, 1846) are reported from the collection made by Mr. J. J. Fougère in 1897. His results have been recalled in some of the immediate works (Hutton 1899; Hudson 1904). Among the main results are the larger size of *X. sobrina* specimens compared to its closely allied *X. zealandica* (McLachlan, 1873) found throughout New Zealand main islands, and other morphological differences observed in the colouration of the first abdominal segment and wing venation. In their studies on the Chatham Islands Alfken (1903), Tillyard (1913) and Wise (1973) report on *X. zealandica* instead of *X. sobrina* and confirm *A. colenisonis*. No morphological records or comments are made in these studies. Macfarlane (1979) establishes *X. zealandica*, *A. colenisonis* and *P. smithii* as very common in the Chatham Islands.



The distributional studies did not discuss the relationship of local Chatham Island fauna to the New Zealand main islands species. Rowe (1981) was the first to pay special attention to the observed differences in size, male appendages and colour pattern of Chatham Island *Xanthocnemis* sp. Unfortunately the material used by Hutton (1898) and Tillyard (1913) could not be examined, but Rowe (1981) believed they belonged to an undescribed species, which is bigger than *X. zealandica* and smaller than *X. sobrina*. Based on the observed differences in shape of the male superior appendage, lateral flanges on the penis and coloration of the thorax Rowe (1981) assigned a new taxon to the Chatham Island *Xanthocnemis* sp. – *X. tuanuii*. He confirmed this view in subsequent work (Rowe 1985, 1987) and considered it as the only representative of the genus on the Chathams. Rowe synonymised all taxa previously reported as *X. sobrina* or *X. zealandica* specimens with the new taxon. Another important finding in his studies on Chatham Island is the high percentage of andromorph (male-like colouration) *X. tuanuii* females and the deviation in colour, shape of the male hamules and size of the genital lobe of *P. smithii* compared with the populations from New Zealand main islands.

Nolan et al. (2007) conducted the most recent study on the Chatham Island Odonata and included molecular analysis on three New Zealand genera – *Xanthocnemis*, *Ischnura* and *Austrolestes*. Nolan et al. (2007) sampled odonates throughout the country, including the Chatham Islands. Eleven allozyme loci and the mitochondrial cytochrome *c*-oxidase subunit I (COI) gene region were used for comparison. Their results are inconsistent with Rowe's findings as far as the genus *Xanthocnemis* is concerned, because both *X. zealandica* and *X. tuanuii* are reported for Chatham Island. However, Nolan et al. (2007) used larvae for their research, which are difficult to distinguish into species based on morphological features alone. Chatham Island larvae identified as *X. zealandica* had an allelic composition similar to that found for this species elsewhere in New Zealand. The only larvae that deviated from this scheme was identified as "presumably *X. tuanuii*". Another striking result of Nolan et al.'s research is the high sequence divergence (COI) between *A. colenisonis* individuals from the Chatham and main islands. Estimates were as high as 3%, approaching a level consistent with species-level differences in other insect taxa.



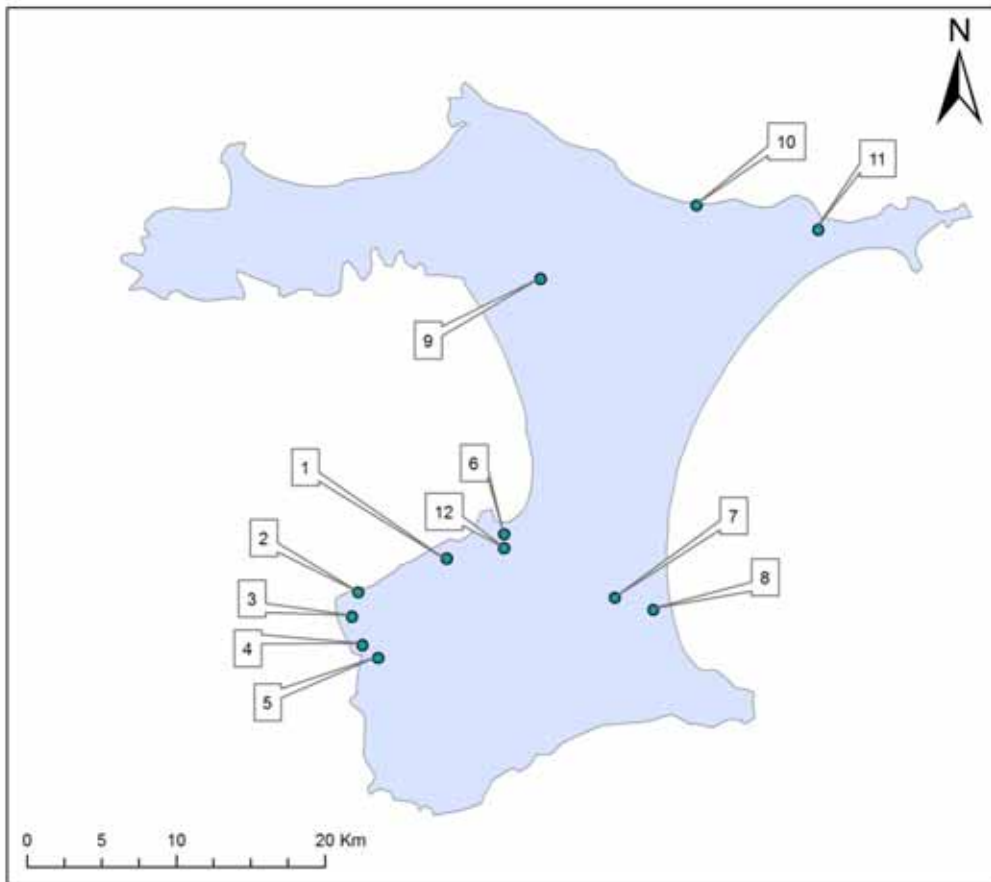
Hebert et al. (2003) give the threshold of 3% as reliable enough to identify 98% of the Lepidoptera species recognised through prior morphological study. It is also compatible with the upper limits of divergence between congeneric Ephemeroptera *Baetica laurentina*/*B. lacustris* and *Caenis latipennis*/*C. youngi* given as 3.8% and 3.3% respectively (Ball et al. 2005). Other mayfly species (*Maccaffertium vicarium*), however, investigated in the same study showed intraspecific divergence of 3.4%.

Considering the previous studies over the Chatham Island Odonata fauna, there is an apparent conflict between the morphological and molecular investigations as far as the genus *Xanthocnemis* is concerned. Morphological investigations proved the existence of *X. tuanuii* as the only species on the island, while molecular analysis established two haplotypes – of *X. zealandica* and “presumably *X. tuanuii*”. No explanation on the possible evolution events was suggested. In addition, more data are needed to identify the taxonomic position of *A. colenisonis* and *P. smithii*. Further, nothing is known about the ecological requirements, behavioural peculiarities and demography of the Chatham Island’s populations. The current study was conducted to fill these knowledge gaps and to contribute towards a greater understanding of the evolution of the insular fauna within the Pacific Ocean. Given the isolation time and the harsh environment on the Chatham Island, which likely constrains reproduction to a short period, it is hypothesised that the observed morphological differences are environmentally driven. In particular, the research seeks to understand the environmental stressors that local odonates are exposed to (low summer temperatures, strong and persistent winds, water chemistry) and which may explain the evolution of the morphological features of those island taxa. It focuses also on morphological and molecular variability of Chatham Island Odonata compared to their South Island counterparts, provides data on the reproductive biology of *X. tuanuii* and provides estimates of demographic parameters (survival, abundance) on Chatham Island. In this paper, the morphological results are provided and commented upon; molecular analyses will be published separately. Taxonomic position of the Chatham Island *A. colenisonis* and *P. smithii* will be dealt with in later studies as well.



Material and Methods

Dragonflies were sampled for one week in January, 2010 on Chatham Island. A total

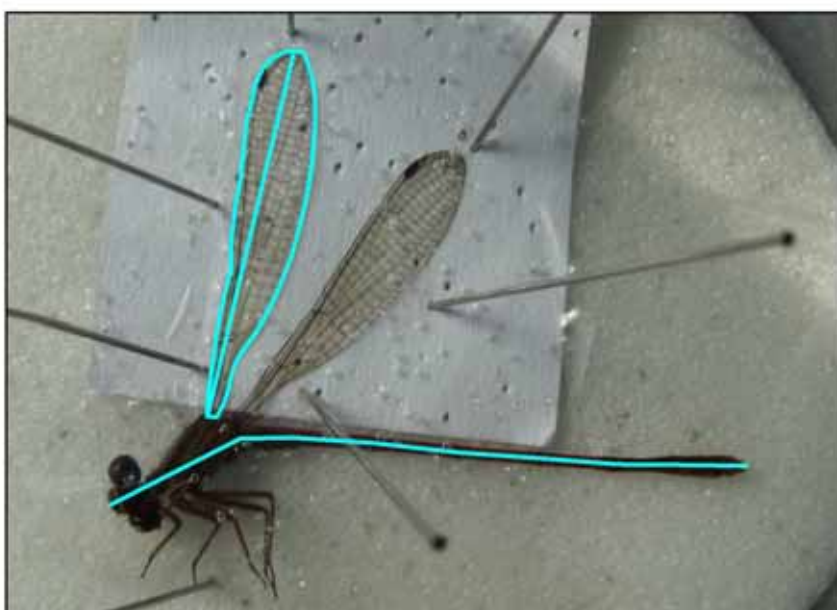


**Figure 2. Sam-
pling localities on
the Chatham Is-
land.**

of 18 localities were visited and odonates were encountered at twelve of them (fig. 2). Eight *X. tuanuii*, eight *A. colenisonis* and seven *P. smithii* were preserved in 90% ethanol

for further DNA analysis.

Morphological features were taken on 77 live individuals belonging to *Xanthocnem-*



is tuanuii and *Austrolestes colenisonis*. They were compared with 47 live individuals sampled from the Canterbury region, the South Island (fig. 3). Each

**Figure 4. *Xanthocnemis tu-
anuii* and *Austrolestes col-
enisonis*: Body/wing mea-
surements. The lines for
measuring distances are
highlighted.**



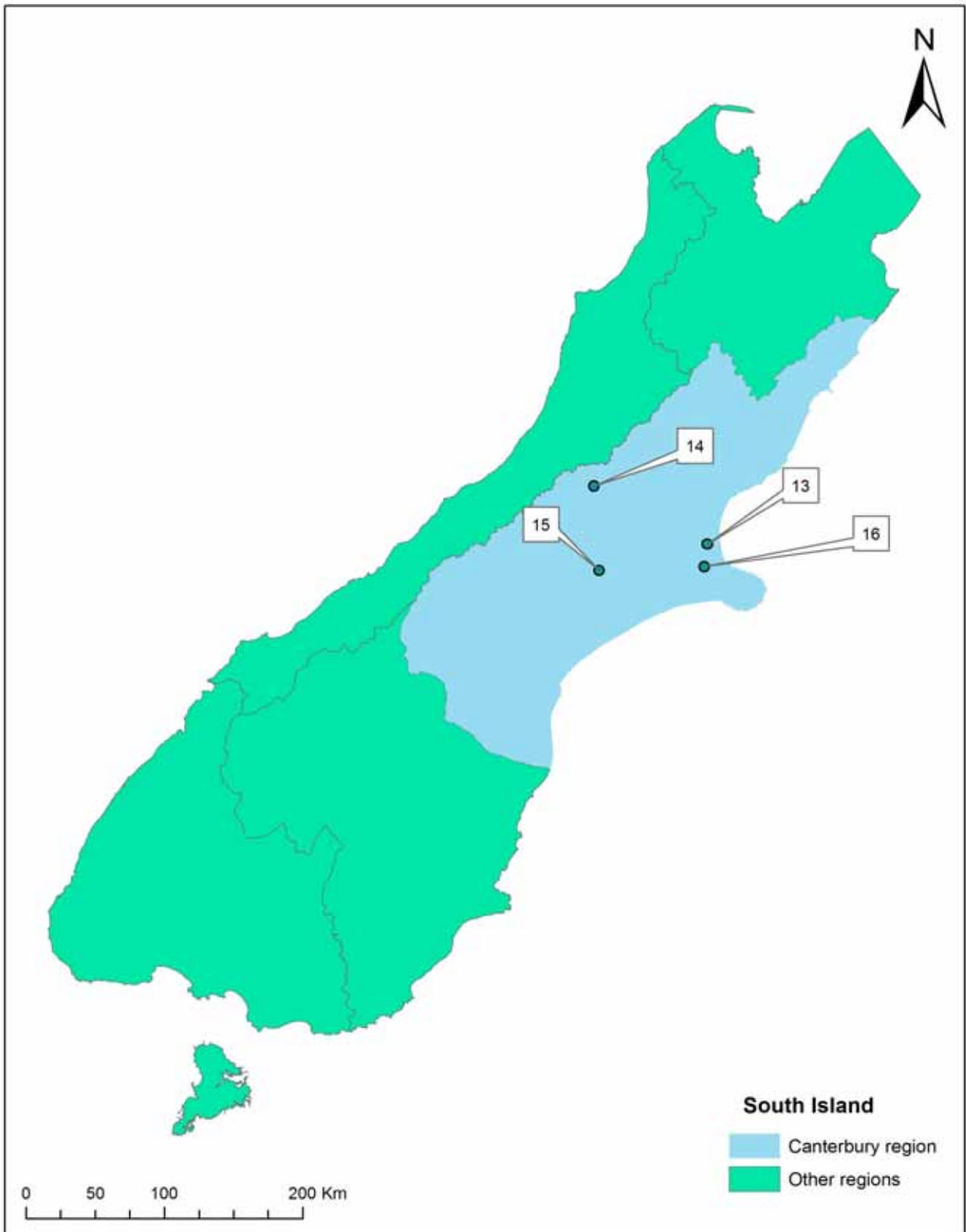


Figure 3. Sampling localities on the South Island.

individual was photographed at a fixed position in front of the objective using a high resolution 10.0 mega pixels camera Fujifilm S1500. The images were processed



in a Geographic Information System (GIS)-environment. This allowed us to measure overall body length, abdomen and wing length as well as wing area (fig. 4). Body length was the distance between the anterior end of the postclypeus and the tip of the anal appendages. Abdomen length was the distance between the anterior end of the first abdominal segment and the tip of the anal appendages. Wing length was measured from the base of the costal vein to the end of the R1 vein in *X. tuanuii* and to the end of R2 vein

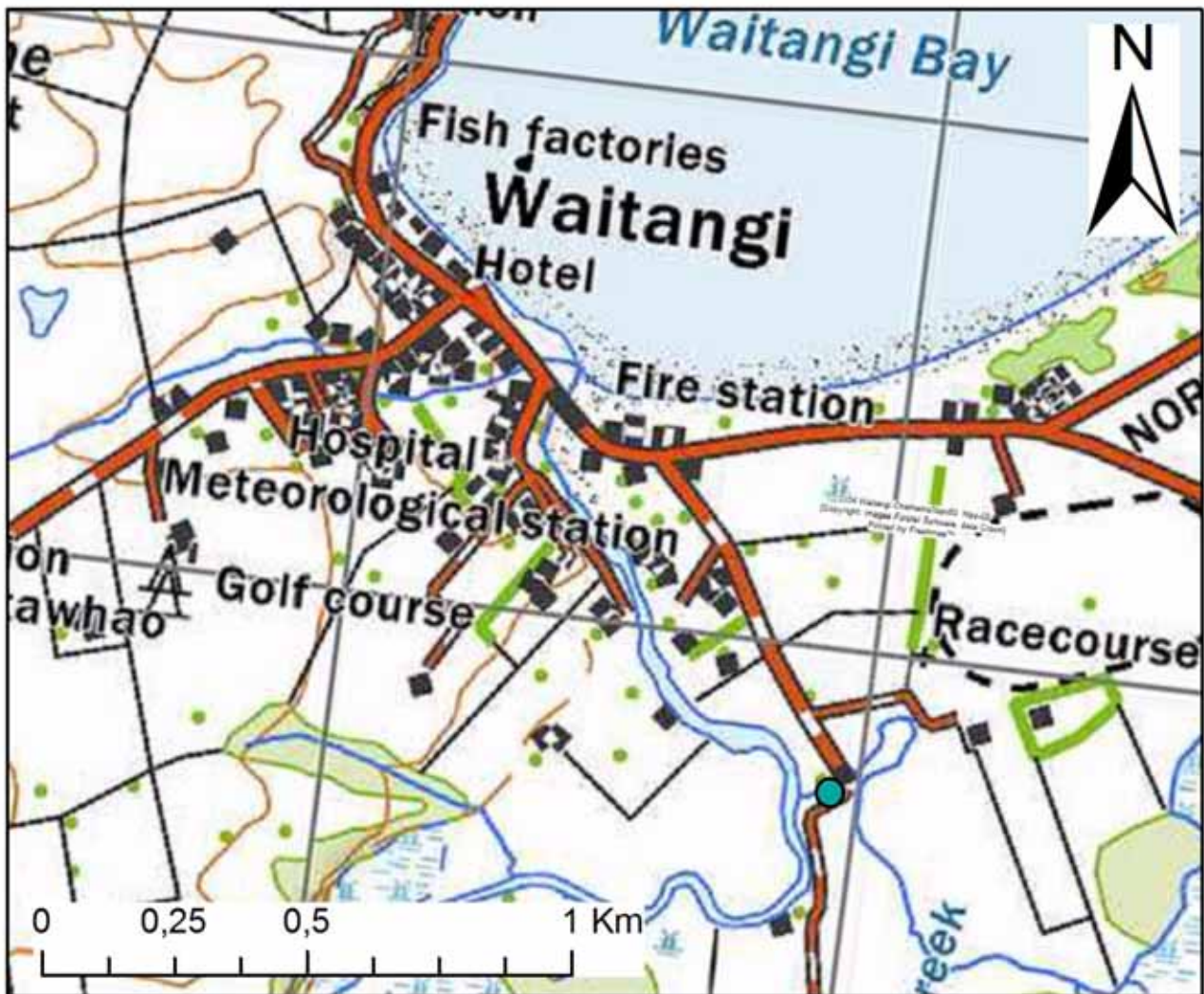


Figure 5. Location of the study site for population analysis at Whangamirno Creek (see blue dot).

in *A. colenonis*. Wing area was the area within the wing margin. All wing measurements were taken from the front wings following Johansson et al. (2009). Three additional variables (ratios) were compared between populations: abdomen to body length



(ab.ratio hereafter), wing length:body length (wing.ratio hereafter), and wing area to wing length (a wing-shape metric). Multivariate Analysis of Variance (MANOVA) was used to statistically compare body-measurement combinations between regions (i.e., Chatham vs. South Island, pooled across localities within each region), followed by post-hoc univariate ANOVAs. For *A. colenisonis*, only males were compared between regions due to low female sample size. All response measures were log transformed prior to analysis in order to satisfy statistical assumptions. To compare overall morphological differences between regions and to visualise them, a Principal Components Analysis (PCA) was performed. The two principal components that explained most of the variation (PC1, PC2) were used.

Morphological comparisons and measurements were also taken from specimens at the Lincoln University Entomology Research Museum. Analyses used the Q Capture Pro software to measure the features shown to be important for species recognition in *X. tuanuii* (Rowe 1985): the black spot overarching the metainfraepisternum below the metathoracic spiracle and the projection of the lower lobe of the male superior appendages. To keep the museum's specimens intact genital structures were not investigated.

A detailed population investigation was conducted within a 50 m long section of Whangamirno Creek about 1.2 km south from Waitangi (fig. 5). The grass vegetation adjacent to the stream (80-90 cm tall) was sampled for adults along a series of set transects that ran perpendicular to the stream. Fixed transects were established for sampling consistency, and to minimise the adverse effects of repeated sampling on *X. tuanuii*'s habitat (i.e., trampling of the grass stems in search of adults). A four day mark-release-recapture (MRR) study was conducted on the following dates: 7, 8, 10 and 11 January. The individuals were marked with Sharpie ultra fine point permanent marker on their right fore-wings, with a unique number applied for each day. Based on the capture histories of marked and released *X. tuanuii* individuals, the daily survival was estimated using the Cormack-Jolly-Seber (CJS) capture-recapture modelling framework (Lebreton et al. 1992). In particular, we modelled survival (ϕ) and recapture probabilities (p) as a function of sex (g) and sample day (t) effects. We distinguished between candidate models using an Akaike's Infor-



mation Criterion model-selection approach (AIC_c , with small sample correction) implemented in Program MARK (White & Burnham 1999). AIC_c is a model selection criterion that balances variation explained with parsimony; we refer the reader to Burnham and Anderson (2002) for a detailed account of this model-selection paradigm. Before fitting models, we assessed whether or not our data met CJS model assumptions (i.e., homogeneity of recapture and survival probabilities among individuals, independence of individual fates, and mark retention/recognition) using the Program RELEASE bootstrap goodness-of-fit test with a model that included all parameters (the saturated model) [i.e., $\phi(g*t), p(s*t)$, following the notation of Lebreton et al. 1992]. Prior to survival estimation, we determined which recapture probability model structure [i.e., $p(g)$, $p(t)$, $p(g*t)$, or the time and sex invariant case, $p(.)$] best described the observed data by fitting four separate models with a constant survival model structure [i.e., $\phi(g*t)$]. The final survival model structure was then selected, and maximum likelihood estimates of parameter values (p and ϕ , and 95% confidence intervals) were obtained. In both model-selection stages, the top model was taken as that with the lowest AIC_c value; models with ΔAIC_c [$\Delta AIC_{ci} = AIC_{ci} - \min(AIC_c)$] values < 2 , however, were regarded as similarly supported by the data. To draw inference on the harshness of the conditions present on the Chatham Islands, we compared survival estimates with published values for odonates in other temperate regions.

We estimated the abundance of *X. tuanuii* in our sampling area using the Jolly-Seber method, which is well suited to cases where populations are demographically open (e.g., organisms die between sampling occasions). Abundance was estimated by maximum likelihood in Program JOLLY (Pollock et al. 1990). Based on the outcome of the survival modelling exercise, Pollock et al. (1990)'s 'Model B' formulation was used, which assumes recapture probability varies but survival is constant across sample occasions; to improve the precision of estimates, we used a combined male-female dataset for this exercise. Estimates (+/- 95% confidence intervals) of daily abundance are presented for our sample site only. Finally, we generated an approximation of island-wide abundance by dividing the mean of daily abundance estimates by the proportion of all suitable Chatham *X. tuanuii* habitats in-



cluded in our survey. For this purpose a predictive habitat model in GIS was constructed based on the behaviour traits and ecological information collected at the time of observation (see below). Land cover shape files for the Chatham and Pitt Islands were included in the analysis. Other Chatham islands, like Mangere, Little Mangere, and Rangatira were not considered as they lack any potential *X. tuanuii* habitats. Only running waters were included as density data for the stagnant water bodies were lacking, and generally those types of wetlands were found to be of lower significance for Odonata species due to increased salinity.

Individual species behaviour was followed during the entire study period with greater details taken from sampling site 1 (see below). A total of 4 hours (between 08:00-12:00) were spent at a section of 30 m along the stream banks. Observation on the warming up behaviour, mating, oviposition (two pairs) and perching distance from the main water body were recorded. Additional records of oviposition were taken from site 11 (numbers not recorded) and site 6 (one underwater and other numbers not recorded). Roosting behaviour was observed at site 9.

Sampling sites on the Chatham Island

1. Matakatau Creek crossing the road Waitangi – Tuku about 4.6 km SW of Waitangi (43°58'45.4''S, 176°35'44.3''W: 31 m a.s.l.): 06th January.
2. Awamata Stream crossing the road Waitangi – Tuku about 11.2 km SW of Waitangi (44°00'20.5''S, 176°39'53.2''W: 21 m a.s.l.): 06th January.
3. Flood by the road Waitangi – Tuku about 13.2 km S of Waitangi (44°01'14.1''S, 176°40'03.4''W: 50 m a.s.l.): 06th January.
4. Little Awatotara Stream crossing the road Waitangi – Tuku about 15.6 km S of Waitangi (44°02'12.3''S, 176°39'22.7''W: 90 m a.s.l.): 06th January.
5. Awatotara Stream crossing the road Waitangi – Tuku about 17.3 km S of Waitangi (44°02'36.7''S, 176°38'32.2''W: 100 m a.s.l.): 06th January.

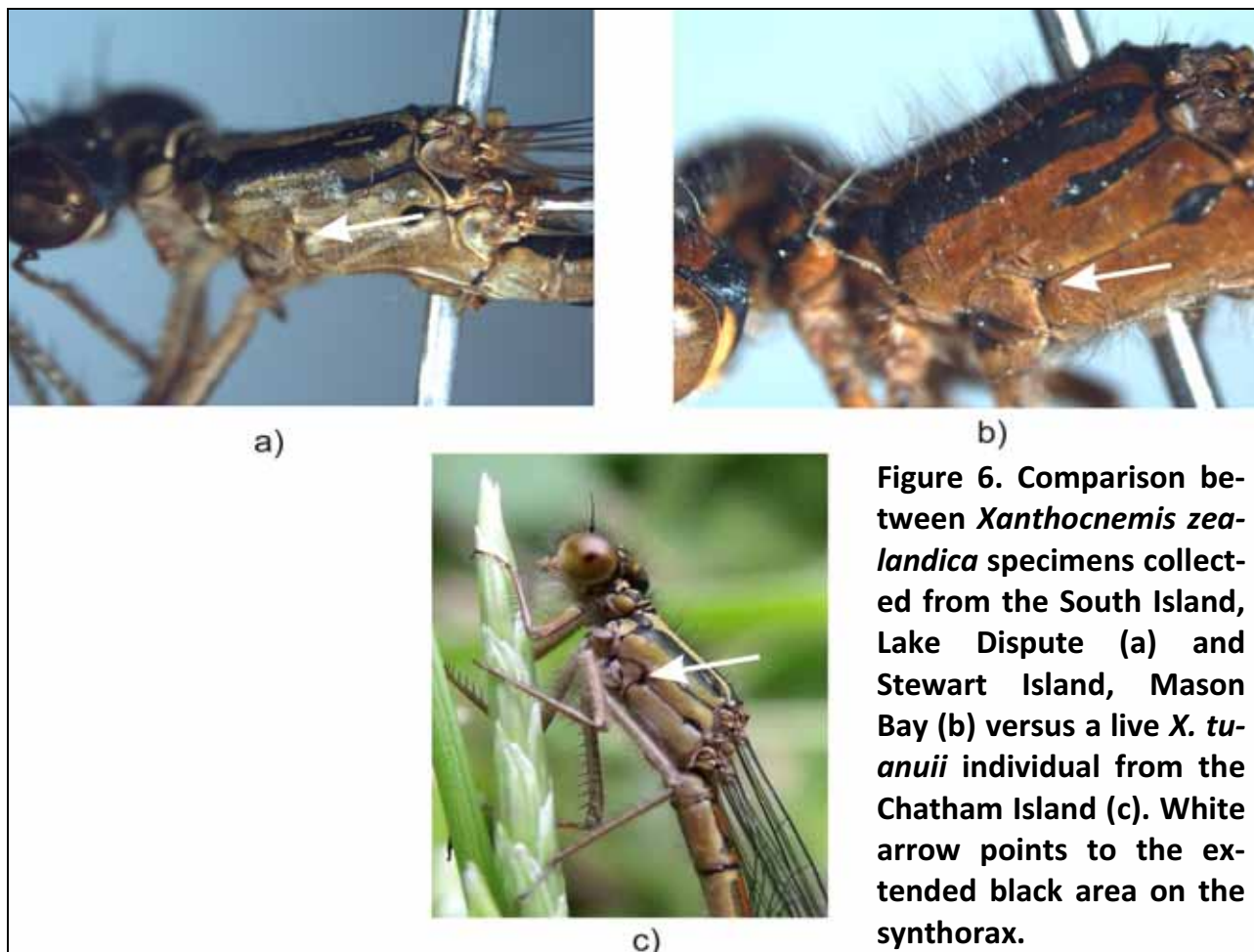


6. Whangamirno Creek about 1.2 km S from Waitangi by the bridge on Matipo Street ($43^{\circ}57'41.7''S$, $176^{\circ}33'04.6''W$: 12 m a.s.l.): 07th, 08th, 10th and 11th January.
7. Te Awainanga River crossing the road Waitangi – Owenga about 11.1 km E of Waitangi ($43^{\circ}59'24.5''S$, $176^{\circ}27'10.7''W$: 9 m a.s.l.): 08th January.
8. Mangahou Creek crossing the road Waitangi – Owenga about 14.1 km E of Waitangi ($43^{\circ}59'41.0''S$, $176^{\circ}22'12.8''W$: 10 m a.s.l.): 08th January.
9. Waimahana Creek crossing the road Waitangi – Wharekauri about 19.5 km N of Waitangi ($43^{\circ}48'21.4''S$, $176^{\circ}32'47.4''W$: 13 m a.s.l.): 08th January.
10. Koomutu Lake roadside by the North Road about 12.7 km E of the junction to Kaingaroa from the road Waitangi – Wharekauri ($43^{\circ}45'03.6''S$, $176^{\circ}25'33.0''W$: 11 m a.s.l.): 09th January.
11. Lake roadside by the North Road about 22.1 km E of the junction to Kaingaroa from the road Waitangi – Wharekauri ($43^{\circ}45'23.4''S$, $176^{\circ}19'25.6''W$: 34 m a.s.l.): 09th January.
12. Bushes roadside by the Matipo Street about 2.2 km S of Waitangi ($43^{\circ}58'08.0''S$, $176^{\circ}32'57.1''W$: 14 m a.s.l.): 10th January.

Sampling sites on the South Island

13. "The Groynes" Recreational area, Christchurch; Riverside grasses ($43^{\circ}27'0.0''S$, $172^{\circ}36'0.0''E$: 15 m a.s.l.): 06th March 2010. *X. zealandica* and *A. colenonis* were sampled.
14. Lagoon Saddle Lake on Cass-Lagoon tramping track ($43^{\circ}03'04.1''S$, $171^{\circ}35'40.1''E$: 1174 m a.s.l.): 25th December 2009. *X. zealandica* was sampled.
15. Irrigation channel passing by the town of Methven ($43^{\circ}37'04.4''S$, $171^{\circ}37'38.3''E$: 346 m a.s.l.): 24th December 2009. *X. zealandica* was sampled.
16. Halswell Quarry Park, Christchurch ($43^{\circ}35'59.1''S$, $172^{\circ}34'27.6''E$: 17 m a.s.l.): 15th November 2009. *X. zealandica* was sampled.





Results

Chatham Island Odonata species list

Three species were found during the study. They are given below with numbers referring to the sampling locality.

***Austrolestes colenisonis* (White, 1846)**

Localities: 6 (7th January), 7, 9, 10, 11, 12.

***Xanthocnemis tuanui* (Rowe, 1981)**

Localities: all localities.

***Procordulia smithii* (White, 1846)**

Localities: 1 (1 exuviae), 8, 9, 11, 12.



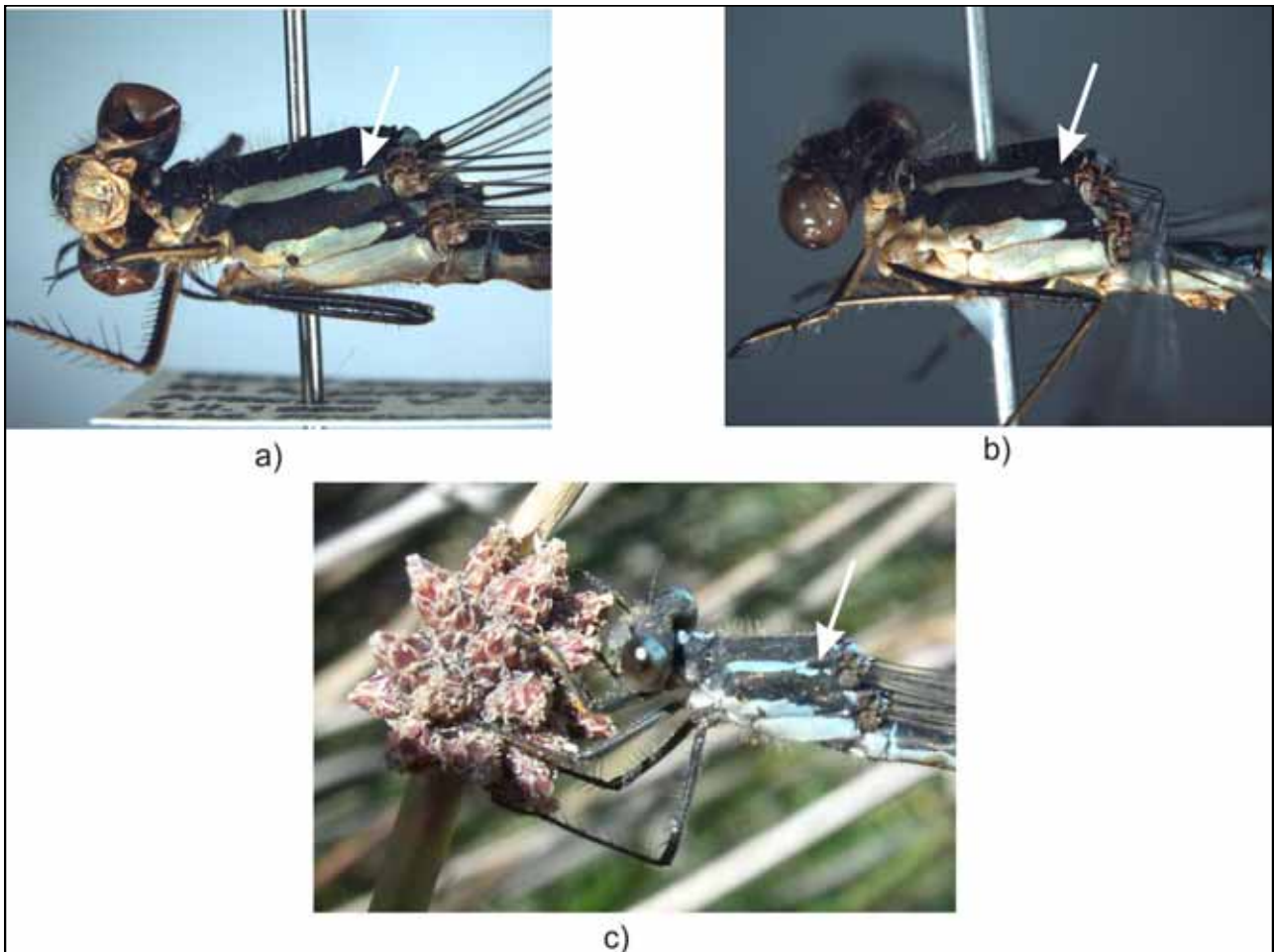


Figure 7. Comparison between *Austrolestes colenisonis* specimens collected from the South Island, Mt. Aspring National Park (a) and Stewart Island, Freshwater Creek (b) versus a live individual from the Chatham Island (c). White arrow points to the extended black area on the synthorax

Morphology

Figure 6 shows the extent of the black area on the thorax of *X. tuanuii* and *X. zealandica* specimens taken from various localities on the New Zealand South and Stewart Islands versus Chatham Island. The dark area in proximity to the metathoracic spiracle, previously considered to be typical of *X. tuanuii* clearly is present in *X. zealandica* as well. Although incomplete, the black regions are partially developed in specimens from Stewart Island. The same tendency was observed in the dark area on the synthorax of *A. colenisonis*. The dark area that interrupts the blue area crosses the line before the base of the wings (Fig. 7). Some specimens from Stewart Island showed no difference in the projection of the lower lobe of male superior ap-



Table 1. Means for body measurement statistics compared between regions for *A. colenisonis* (A.c.) and *X. zealandica/tuanuii* (X.z.). Response variables differing significantly between regions (within-sexes) are denoted by gray coloured cells. Sex: male (m), female (f)

Species	Sex	Region	Abdomen Length (cm)	Body Length (cm)	Wing Length (cm)	Wing Area (cm ²)	Abdomen: Body Length	Wing: Body Length Ratio	Wing Area: Length Ratio
A.c.	m	Chat-ham	3.59	4.52	2.52	0.83	0.79	0.56	0.33
		South Isl.	3.63	4.50	2.51	0.79	0.81	0.56	0.32
X.z.	f	Chat-ham	2.61	3.38	2.11	0.58	0.77	0.62	0.27
		South Isl.	2.47	3.07	1.92	0.47	0.80	0.62	0.25
	m	Chat-ham	2.67	3.45	1.98	0.52	0.77	0.57	0.26
		South Isl.	2.48	3.14	1.82	0.43	0.79	0.58	0.24

pendages when compared to Chatham Island specimens (fig. 8). Due to the small

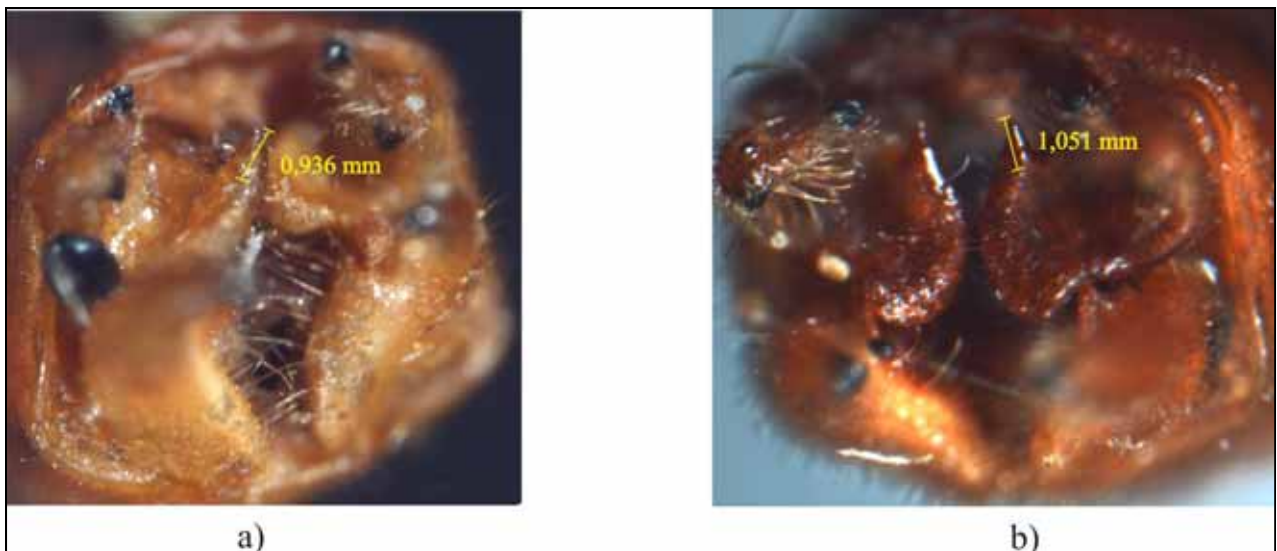


Figure 8. Comparison between *Xanthocnemis zealandica* specimen collected from the Stewart Island, Mason Bay (a) versus *X. tuanuii* from the Pitt Island (b). Measurements are taken on projection of the lower lobe of the superior appendages.



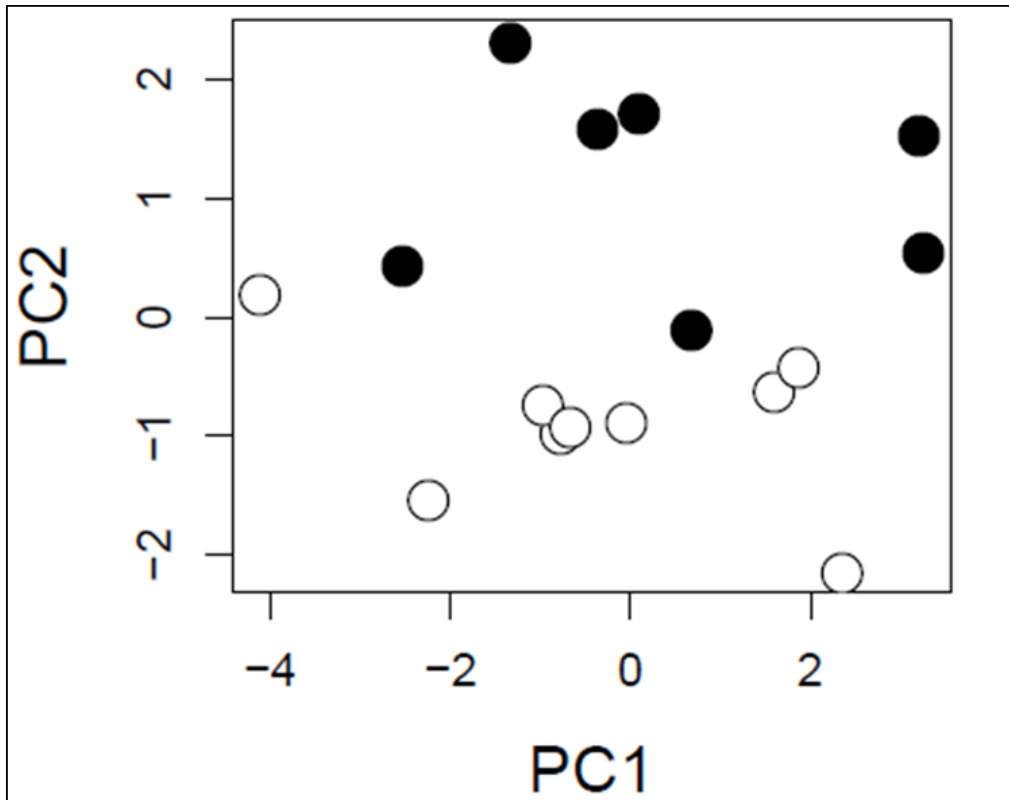


Figure 9. Principal components analysis of morphological measurements for Chatham Island (white circles) and South Island (black circles) *Austrolestes colenisonis* males. PC1 is negatively correlated with all body size metrics (body, abdomen, and wing lengths; wing area), whereas PC2 is negatively

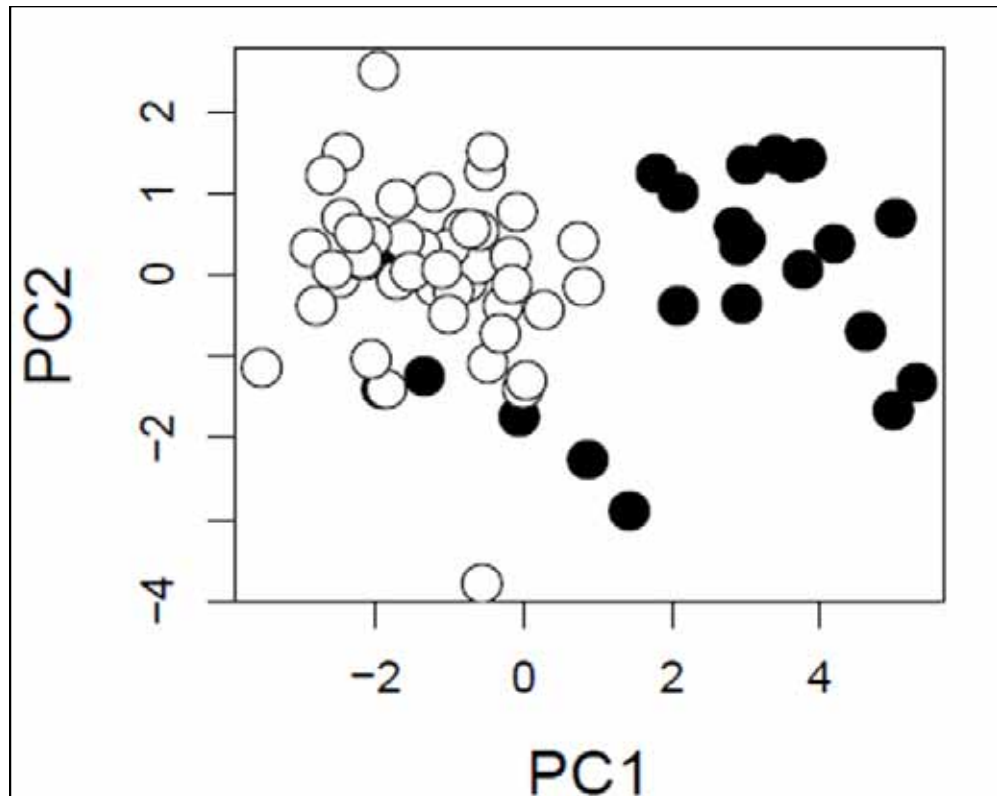
correlated with the abdomen : body length ratio. MANOVA indicated that *A.colenisonis* morphology differed significantly between the two regions ($F_{4,11} = 16.5$, $P < 0.001$), with post-hoc univariate ANOVAs demonstrating regional abdomen:body length ratio and wing shape (i.e., wing area:wing length ratio) differences ($P < 0.05$ for both); there were no significant differences for other metrics ($P > 0.10$ for all).

sample size from Chatham Island this result was not numerically tested.

Both sexes of *X. tuanuii/zealandica* and male *A. colenisonis* differed significantly in their overall morphology (principal components) (fig. 9-11; $P < 0.001$ for all). In particular, Chatham Island *X. tuanuii* were significantly larger, had relatively broader wings (wing-shape metric) and possessed a relatively smaller abdomen per body length (ab.ratio) than their South Island counterparts. This result was observed for both males and females ($P < 0.05$ for post-hoc univariate ANOVAs). Given the body-size scaling relationships for both the wing-shape metric and ab.ratio, all *X. tuanuii/zealandica* morphometric differences were driven by size differences. In contrast, *A. colenisonis* differed between regions in wing-shape and ab.ratio ($P < 0.05$ for both post-hoc univariate ANOVAs), but was similar in overall size (body length, abdomen length, wing length, and wing area; $P > 0.05$ for all). There was no difference in wing.ratio for either species or sex between regions (Table 1).



Figure 10. Principal components analysis of morphological measurements for Chatham Island (white circles) and South Island (black circles) *Xanthocnemis tuanuii/zealandica* males. PC1 is negatively correlated with all body size metrics (body, wing and abdomen, lengths; wing area) and the index of wing



shape, whereas PC2 is negatively associated with the ratio of wing:body length only. MANOVA indicated that *X. tuanuii/zealandica* morphology differed significantly between the two regions ($F_{4,64} = 25.5$, $P < 0.001$); post-hoc univariate ANOVAs indicate that males in the two regions differed significantly in all morphological dimensions ($P < 0.001$ for all) except with wing:body length ratio. The index of wing shape, whereas PC2 is negatively associated with the ratio of wing:body length only. MANOVA indicated that *X. tuanuii/zealandica* morphology differed significantly between the two regions ($F_{4,64} = 25.5$, $P < 0.001$); post-hoc univariate ANOVAs indicate that males in the two regions differed significantly in all morphological dimensions ($P < 0.001$ for all) except with wing:body length ratio.

Plots of PC1 vs. PC2 clearly depict these patterns of morphological separation between South Island and Chatham Island *X. tuanuii/zealandica* and male *A. colenso-nis* populations (fig. 9-11).

Female colour polymorphism of Xanthocnemis tuanuii

Female *X. tuanuii* were found to be highly variable in colour with almost every individual possessing a unique combination of black and red spots. Figure 12 shows



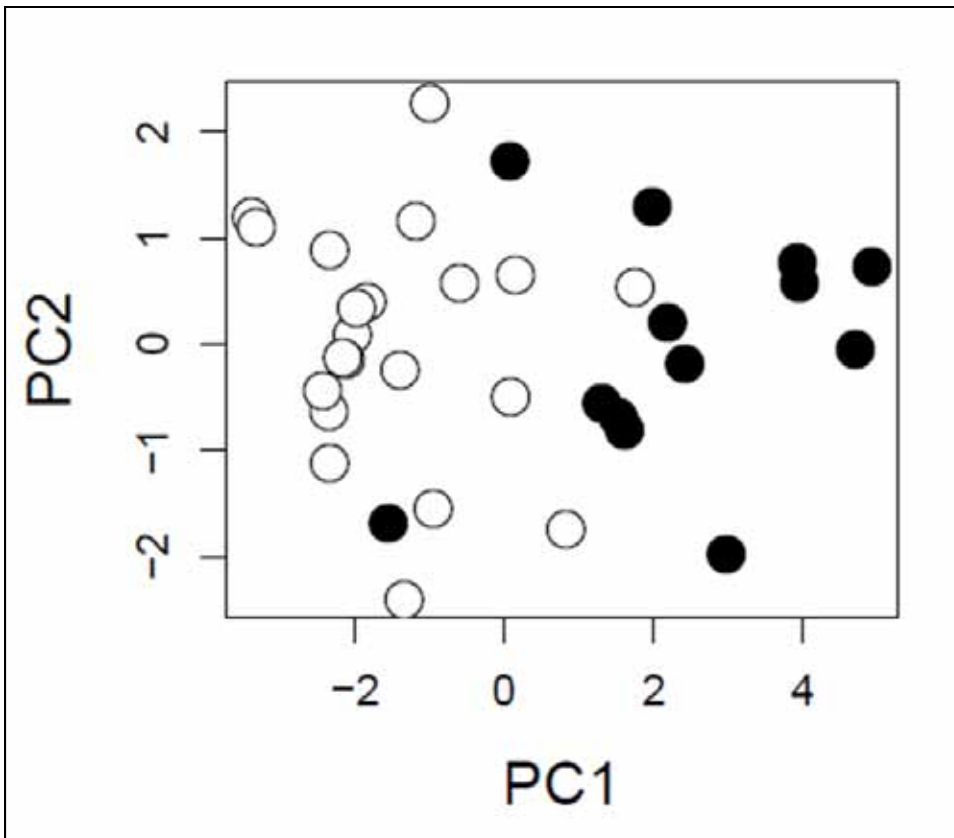


Figure 11. Principal components analysis of morphological measurements for Chatham Island (white circles) and South Island (black circles) *Xanthocnemis tuanuii/zealandica* females. PC1 is negatively correlated with all body size metrics (body, abdomen, and wing lengths; wing area), whereas PC2 is negatively associated with wing area and positively associated

with abdomen lengths. MANOVA indicated that *X. tuanuii/zealandica* morphology differed significantly between the two regions ($F_{4,29} = 21.2$, $P < 0.001$); post-hoc univariate ANOVAs indicate that males in the two regions differed significantly in all morphological dimensions ($P < 0.001$ for all) except with wing:body length ratio.

some examples of the patterns encountered within the Chatham Island population.

Table 2. Total area covered by the red colour in *X. tuanuii* females.

Extension of red area	Number within population	Percentage
totally black	17	29,83
abdominal segment 2 (S2)	6	10,53
abdominal segment 3 (S3)	5	8,77
abdominal segment 4 (S4)	4	7,02
abdominal segment 5 (S5)	14	24,56
abdominal segment 6 (S6)	7	12,28
abdominal segment 7 (S7)	1	1,75
abdominal segment 8 (S8)	3	5,26



Figure 12. Colour polymorphism in females *Xanthocnemis tuanuii*. Specimens are group based on the extent of the red area. Two males are given for comparison. [The colour of the females' appendages should not be taken as reference for future studies. It is wrong for most of the forms as was not so well visible on the pictures taken on live individuals.]

They are grouped according to the size of the red areas over the dorsal surface. A clear distinction between *andromorphs* (resembling male colouration) and *heteromorphs* (differing from males) could not be made because the observed colour variation was gradual on the abdominal segments S1 to S8. Greater variations of the red spread are observed for S3-S5. Examples are displayed on fig. 12 and table 2. The latter was produced based on data taken at the population estimation site only, while fig. 12 includes data taken from the whole island.

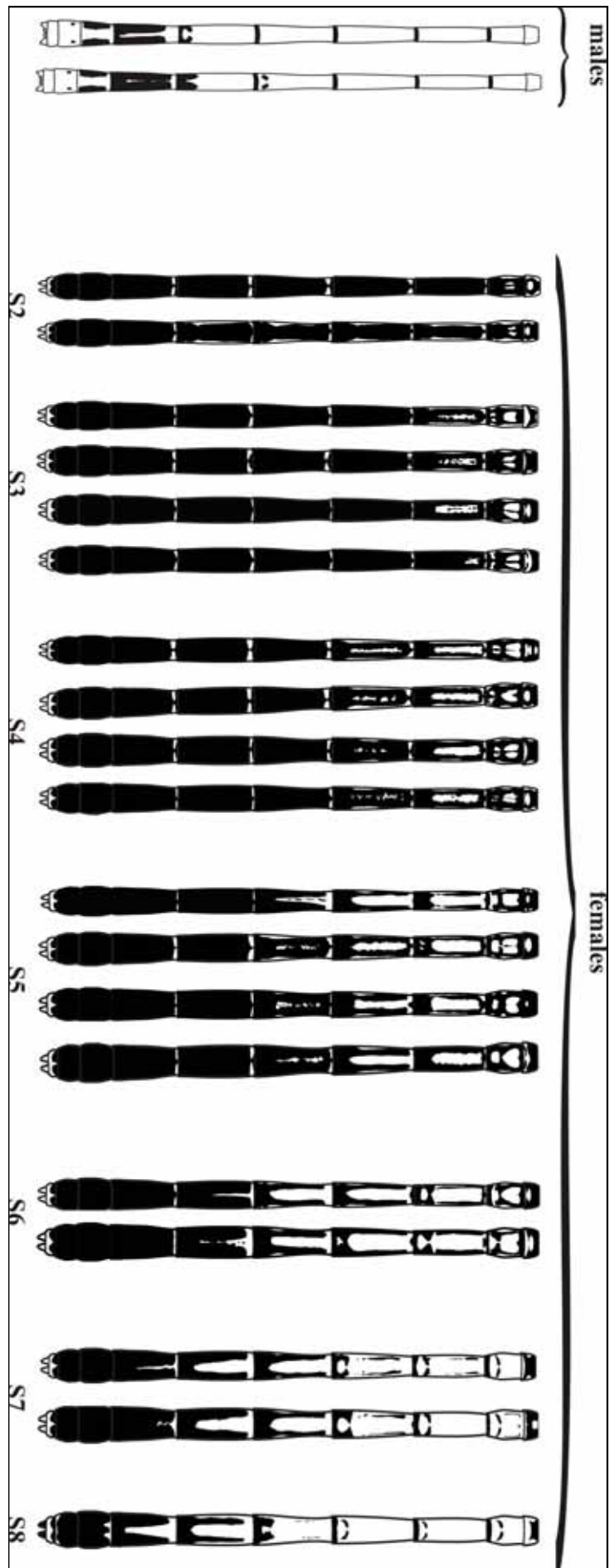




Figure 13. Males *Xanthocnemis tuanuii* perch close each other.

Behavioural notes on Xanthocnemis tuanuii

Chatham Island odonates were encountered predominantly in sheltered sites, like vegetation belts along the wetland bank and adjacent grasses, as well on the sloped upper banks of streams. In those areas, *X. tuanuii* stayed inactive until the air temperature increased to about 16°C, which could happen as late in the morning as 10:00 am. Prior to this time, if disturbed, adults moved in a very slow mode crawling on the plant stems or flying short distances usually up the tree tops, deep in the vegetation or low down between the grass stems. The first activities during the day were usually males appearing near the water edge where they perched on floating *Potamogeton* sp. leaves, submerged stems, or directly on the stones. Aggressive interactions between conspecific males were common and very strongly demonstrated at the water edge or among the grasses. However two males showing little apparent aggression and sitting next to each other on a stone above water were ob-





Figure 14. *Xanthocnemis tuanuii* exuviae among dense grass vegetation.

served as well (fig. 13). On a single occasion, aggressiveness was observed between a male *X. tuanuii* towards a passing male *P. smithii*. Despite being aggressive, the males seemed not to be territorial as they were not seen returning to the same perching place after initiating an attack.

A notable increase in activity was observed in late morning, when air temperatures rose to 19°C. Males occupied areas around the water's edge or perched on floating leaves with their heads orientated downstream. Single individuals were found to fly as far as 400 m from the water and stay perched on the short vegetation even if the site lacked shelter. The first tandems were observed at the water edge at late morning, too. Some of them had apparently already formed away from the water, as they arrived at the study area already in tandem, while others formed over the water surface. On one occasion, an already-formed tandem stayed on grasses above water for about 2-3 minutes and flew to the nearest bush at a height of about 2 m. The copulation wheel was formed there and they



stayed in this position for about 2:30 minutes. Copulating pairs were observed above the water surface and up to 44 m from the actual oviposition area. Females



Figure 15. Marked male *Xanthocnemis tuanuii* holding unmarked female.



laid eggs guarded and ovipositing couples were observed perching very close to each other. Males did not necessarily stay with their partners during post-copulation activities. They could abandon the females some seconds before she finished egg-laying. A single observation was made of an underwater oviposition. The couple submerged, but the male left the female to lay eggs alone under the water. The total duration was not followed, as the female was disturbed after 13 minutes. She stayed below the surface at about 30 cm and was not visible from the stream bank due to the very turbid water.

Emergence was observed at late morning around 11:20 am. About 8 cm above the water surface was the lowest level of emergence observed at this site. Other exuviae collected from the same site were found on the plant stems (sometimes around the top) to a mean height of about 27.2 cm (N=13; maximum at 57 cm). Most of the exuviae were very well hidden among the vegetation and difficult to find (fig. 14). Larvae could also use bridge walls as substrate for emergence to a mean height of about 37.4 cm (N=7; maximum at 87 cm and minimum at the stones near the water edge). Another late emergence took place at 1.36 pm. Teneral used dense bank vegetation, stayed about 3 m away from water edge inside the tree belts, or hid among single *Juncus* sp. tufts distanced about 5 m from the stream. Mostly males occurred at the stream banks and nearby grasses (80-90 cm high). At these grasses adults were observed "diving" and flying between the stems for short distances before perching. Solitary females were very rarely seen at the same places unless the area was already abandoned by males. That occurred around 6:30 pm during the period of observation. Around the same time their activity dropped down significantly. The individuals showed site attachment and did not fly away after being caught and released at their potential roosting places. Adults spent the night in bushes approximately 40 m from the stream.

Survival and abundance of Xanthocnemis tuanuii

The marks applied to individuals appeared to have had no effect on their behaviour. For example, we frequently observed tandems between marked and unmarked in-



dividuals in various combinations at the study site (fig. 15). Similarly, aggressive behaviour was initiated by marked individuals towards unmarked, and vice versa.

Table 3. Model-selection results for *Xanthocnemis tuanuii* Cormack-Jolly-Seber survival analysis. All models were fitted with a time-varying recapture probability model structure. K is the number of estimated parameters. All notation follows Lebreton et al. (1992): ϕ and p are survival and recapture probability, respectively, whereas g is group (sex), t is time, and $g*t$ is their interaction.

Model	Description	AIC _c	ΔAIC _c	K	Devi-
$\phi(g) p(t)$	Survival varies by group, but not time	236.3	0	5	14.0
$\phi(.) p(t)$	Survival is constant across groups and time	237.5	1.3	4	17.4
$\phi(t) p(t)$	Survival is constant across groups, but varies in time	238.3	2.1	5	16.1
$\phi(g*t) p(t)$	Survival varies by group and time	240.0	3.7	8	11.3

Demographic parameters were estimated based on the capture histories of 218 *X. tuanuii* individuals, three quarters of which were male ($n = 162$ males, $n = 56$ females). Program RELEASE bootstrap goodness-of-fit test results suggest that the CJS model adequately fit our data ($n = 100$ simulations, $P = 0.69$). Recapture patterns provided similar support for a recapture model that was either fully saturated (i.e., with both time- and sex-specific estimates of p ; lowest AIC_c or $\Delta AIC_c = 0$) or time dependent ($\Delta AIC_c =$

Date	N	Var(N)	SE(N)	95% CI
7 Jan	-	-	-	-
8 Jan	329	11,277	106	121-537
10 Jan	280	13,776	117	50-510
11 Jan	298	10,335	102	99-497
Mean	302	-	-	-

Table 4. Maximum likelihood estimates of daily abundance (N) for *X. tuanuii* (males and females combined). Estimates were generated using Program JOLLY with the 'Model B' formulation (i.e., constant survival, time-varying recapture probability) of Pollock et al. (1991).



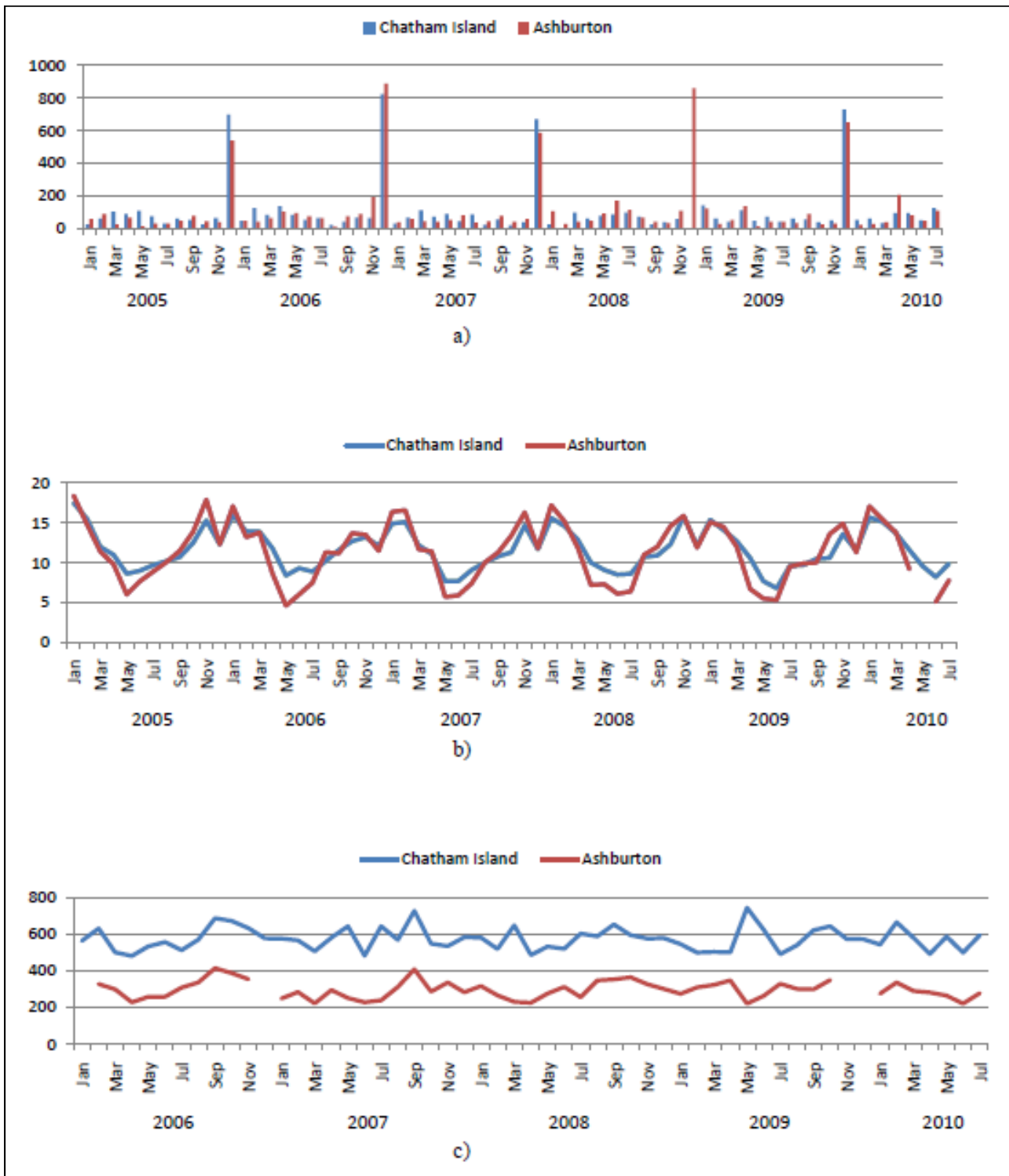


Figure 16. Comparison of the climatic situation between the Chatham Island and the South Island – vicinity of Ashburton. Description of units: a) total rainfall (mm); b) mean air temperature (Celsius); c) mean daily wind run (Km).

0.4). Given this tie, we pursued survival model selection using the recapture structure with fewer parameters [i.e., $p(t)$]. *X. tuanuii* survival was constant across days, and model selection results were suggestive of a between-sex survival difference



[i.e., $\phi(g)$, $p(t)$ was the top model; table 3]. However, since AIC_c for the next-best model was within 2.0 ΔAIC_c units of this model, statistical support for a sex effect was modest at best. Based on the top model, daily survival for males (0.75; 95% CI: 0.49-0.91) was 50% higher than what was estimated for females (0.50; 0.23-0.77), though confidence intervals overlapped substantially for these groups; recapture



Figure 17. Tree vegetation influenced by the winds on the Chatham Island.

probability averaged 0.21 (range: 0.13-0.34) across sample days.

Using our capture-recapture dataset, we estimated that in total 302 adult *X. tuanuii* occurred in our 2,000 m² study area, on average (table 4). Due to a relatively modest recapture probability (i.e., mean of 0.21), however, the precision of daily abundance estimates was relatively low. Using GIS, we estimated that an additional 41 km² of potentially suitable *X. tuanuii* habitat (22 km² riparian areas along flowing waters, and 19 km² upper banks of rivers) was available on both Chatham and Pitt islands; our study site thus comprised 0.03 % of available habitat. Assuming abundance patterns at our site are representative of what can be found elsewhere, we



estimate that 3.3 million and 2.9 million individuals could occur along running water habitats and on slope areas near streams, respectively. Thus, over 6.0 million individuals may occur on the two islands in total, which is a coarse approximation of the total world population of this species.



Figure 18. Brown water stream typical of the Chatham Island.

Discussion

Chatham Island has a characteristic environment, which Rutledge (1992) identifies as cool, cloudy and windswept, with a temperature range between about 5°C in the winter and 18°C in the summer. Compared to an area situated at the same latitude on South Island (vicinity of Ashburton), temperature is lower, winds are stronger and there is more precipitation on Chatham Island (data from 2005 to present: National Institute for Water and Atmospheric Research (NIWA) <http://cliflo.niwa.co.nz/>) (fig. 16). The temperature threshold of 12-12.9°C given as a start for the flying season of many species living in the temperate zone (Belyshev et al. 1989, Cor-



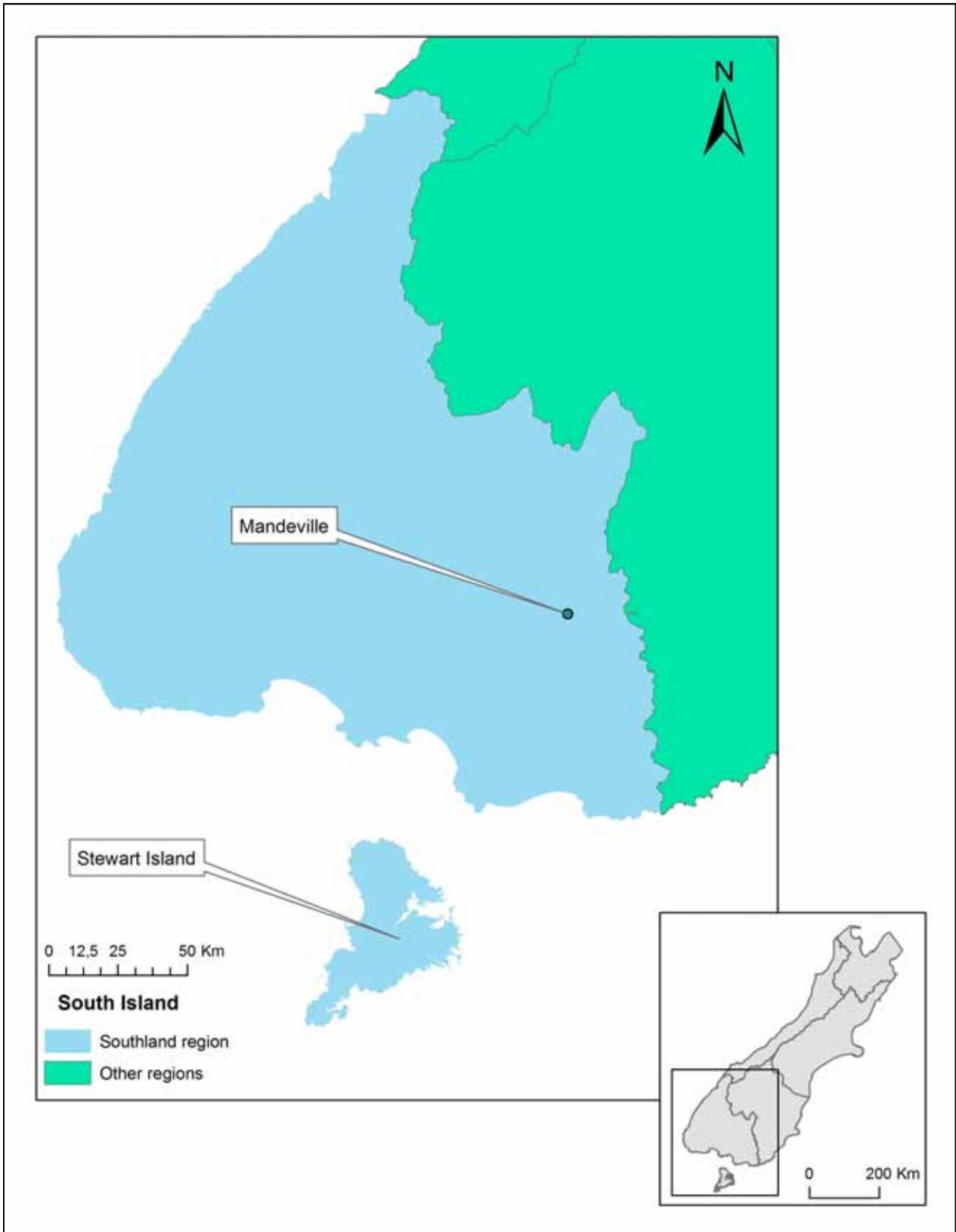


Figure 19. Location of Mandeville, Southland region, the South Island.

bet 1999) is reached for both regions about September-October. Thereafter, the mean air temperature over Ashburton stays higher nearly for the whole flying sea-



son, which is generally up to April. The temperature difference displayed on figure 16 may not seem so significant, however in combination with the constant winds blowing on the Chatham Island (cf. fig. 16, c) could be quite influential (cf. fig. 17 for wind effects on trees). Brown stream waters are another peculiarity of the Chatham Island (fig. 18). Previous research from the New Zealand West Coast area found that such colour is normally associated with low pH of about 4, which results from acids derived from decaying vegetation (Winterbourn & Collier 1987). Low pH values are limiting for many odonate species (Corbet 1999).

In summary, Chatham Island represents harsh environments for Odonata. Within the framework of the present study, a few morphological and behavioural traits may be hypothesized to have evolved in response to such conditions. Few could be pointed out as results of the current study: dark areas over the body, larger wing area, relatively shorter abdomen in proportion to the total body length, female colour polymorphism and underwater oviposition.

Body morphology

The morphological analysis shows that Chatham Island and the South Island *Xanthocnemis* species do not differ in the shape of the lower lobe of the male superior appendages, which is given as the main character to distinguish between the members of the genus (Rowe 1985). Specimens with sharp pointed projections, typical of *X. tuanuii*, are found from the Stewart Island, too. A similar finding was reported earlier by Rowe (1985) from the area of Mandeville, Southland region (fig. 19). The black area overarching the metainfraepisternum below the metathoracic spiracle is another feature used to identify *X. tuanuii*. It is, however, not typical of individuals from the Chatham Island only. Although weakly developed, it has been observed in specimens collected from the Stewart Island as well. Its possible function in relation to the environment is discussed below alongside the only significant morphological differences observed in certain proportions.



Colour is considered as one of the mechanisms which dragonflies use to regulate their body temperature (Corbet 1999): "Heat exchange [with the environment] takes place ... at a rate that depends on the temperature difference between the insect and its surroundings; on its surface area, orientation and shape, pubescence, and (for radiation) colour and pruinescence". This relationship may explain the darker area exhibited by Chatham Island *X. tuanuii* and Stewart Island *X. zealandica* (the same tendency of darker thoracic area is observed in Chatham and Stewart Island *A. colenisonis* as well). The fact that black colour particularly developed around the thoracic spiracle suggest a possible advantage in thermoregulation in those animals. The role of the thoracic temperature for the pre-flight warm up of the entire body is suggested by May (1976). Its mechanism is revealed by Heinrich & Casey (1978). As the heat transfer occurs via haemolymph pumped from the thorax to the abdomen it is possible that dark areas around the spiracles (through which external air reaches the inner thorax) are beneficial for this heat transport. It is especially important for so called 'perchers' (after Corbet 1962), to which both *X. tuanuii* and *A. colenisonis* belong. Being small-sized, they depend more on the air temperature (De Marco et al. 2005) than active fliers, which can also regulate their body temperature endothermically (Corbet 1999).

Wing surface area is another factor that may have been shaped by natural selection. Larger wings observed on Chatham Island individuals could be a result of the inferred here longer pre-imaginal development, the winds constantly blowing on the island or a combination of both. Larger body length on Chatham compared to South Island individuals is demonstrated here only in *X. tuanuii*. It is, however, a well proved feature of species living in higher latitude regions. Johansson (2003), for example, established that a latitudinal shift in body size of *Enallagma cyathigerum* (Charpentier, 1840) was caused by larval development. Longer development resulted in larger sized adults. This effect, however, is very significant in *X. tuanuii*, which has a larger body, but a relatively shorter abdomen per body length (cf. ab.ratio). A possible explanation is the proportional development of the thoracic capsule to cope with the increased wing load. It is a commonly established phenomenon for the insects living under high pressure of the blowing winds to re-



duce or completely lose their wings and Chatham island beetle fauna is a good example. Emberson (1995) reports about 90% of the endemic Coleoptera as being flightless. Odonates, however, cannot respond to the winds by reducing their wing masses, as the flight is their only means for dispersal. In this connection Johansson et al. (2009) established that the ubiquitous migratory species, like *Pantala flavescens* and *Tramea* sp. have certain areas of their hind wings enlarged in order to cope with the environmental conditions during the long distance dispersal. The strong winds blowing over the vast ocean surfaces are definitely among the challenges that those species face during migration.

Female colour polymorphism

Female colour polymorphism is widely distributed and well documented among Odonata. Fincke et al (2005) report on 144 Holarctic polymorphic taxa (in 134 spp.) with the family Coenagrionidae being the most striking example of diverse female morphs. Usually two distinct forms are encountered – andromorphs and heteromorphs – with some intermediates observed in variations of the light colour and black patterning. The dichotomy in this character is well represented, as only 13% of the Holarctic polymorphic species have more than two morph types and 4% are polymorphic but lack a female morph that resembles the conspecific male (Fincke et al. 2005).

Many investigations have been carried out to explain the basis for the female colour polymorphism, particularly the existence of andromorphs. In spite of the number of theories (reviewed in Joop 2005), the maintenance of the colour morphs among the populations and its functional importance are still an open issue (Joop et al. 2007). Various studies evidence that female morphs may not be significantly different in lifetime fitness correlates (Fincke 1994), clutch or egg size (Joop et al. 2007), survival and recapture rates (Van Gossum et al. 2004). Differences are observed in egg shape (Joop et al. 2007), sperm storage capacity (Van Gossum et al. 2005a), male harassment depending upon the frequency (Van Gossum et al. 2005b), and in certain occasions in reproductive success (Takahashi & Watanabe



2010). Joop (2005) purports that colour polymorphism might be related to immune function and provides evidences for this assumption.

The present study reports an interesting pattern of variation in female colour polymorphism in nature. Previous studies on Chatham Island (Rowe 1981, 1987) report on high frequency of andromorphs *X. tuanuii* without specifying the type of colour pattern over the females' bodies. One may assume that the author refers to all females with some patches of red areas as being andromorphs and only those with totally dark dorsal abdominal surface as heteromorphs. The present study demonstrates for the Chatham Island a situation that is rarely found in other populations. The variation in female colouring is very high and it is almost impossible to assign a female to a specific morph. Thus, the data show that andromorphs may represent one end of a whole spectrum, rather than distinct separate morphs. The problem is in choosing the right criteria – should it be the red colour regardless of the occupancy over the body or the black pattern, or combination of both (commented in Joop 2005)? If the first criterion is selected, then the andromorphs are quite common (70.17% of all females) and prevail over heteromorphs in the studied population. However, Fincke (2004), following Walker (1953), suggests that in populations with highly variable colour pattern due to intermediate forms, andromorph must refer to the most extreme case, which is S8-type females. In the present case, this would include 5.26% of the females studied population from Chatham Island (fig. 12). Other females should be considered as heteromorphs although the red area is progressively developing over the abdomen dorsum. It would be interesting to see whether studies that report female colour polymorphism and are based on low sample sizes would also show a more continuous variation if the sample size were increased.

Van Gossum et al. (2001) argue that female morph frequencies may also vary on a temporal and on a spatial scale. The final conclusion upon the extent of female colour polymorphism in *X. tuanuii* should, therefore, await more intensified investigations over the entire flying season, which is for now considered to be January-February. Given the fact that the female *X. tuanuii* is an imperfect mimic (after Sherratt 2002) and does not resemble so closely the typical male body pattern (cf.



fig. 12), more detailed studies may also result in more precise estimates of andromorph vs. heteromorph females.

One could argue that in addition to the above mentioned selection pressure, the polymorphism in nature is maintained by the composite influence of the environment. *X. tuanuii* is a good example to demonstrate such phenomenon. The high pressure from the harsh environmental situation on the Chatham Island (see above) requires development of specific morphological features and behavioural traits, which are possibly not embedded in the population due to an inferred here incomplete lineage sorting.

Joop (2005) shows that the body colour changes with temperature. She also suggests that males *Coenagrion puella* (Linnaeus, 1758) develop less black over their body compared to females as a consequence to longer exposure to higher temperatures. Females usually stay away from water (respectively from incident sun light) hidden in the vegetation, which agrees also with the observed behavioural pattern in *X. tuanuii*. Solitary females were encountered mainly at the marginal grass zones avoided by males or near the water at late afternoon when the territory is abandoned by males. Chatham Island's mean summer temperature of just 18°C perhaps additionally contributes to the persistence of the black coloration over the female bodies.

Underwater oviposition

The observation of underwater oviposition on a single occasion is perhaps another indication of the pressure imposed on females by extreme weather. For example, Fincke (1986), for *Enallagma hageni* (Walsh, 1863), suggests a selective advantage of underwater oviposition that by doing so females: a) decrease the risk of their eggs desiccating, and b) avoid the interruption of oviposition by wind and rival males. At the Chatham Island, the former danger is excluded. Females possibly acquire this oviposition mode in occasions of strong winds, which is persistent over the island, or in response to male pressure because it was not observed on a regu-



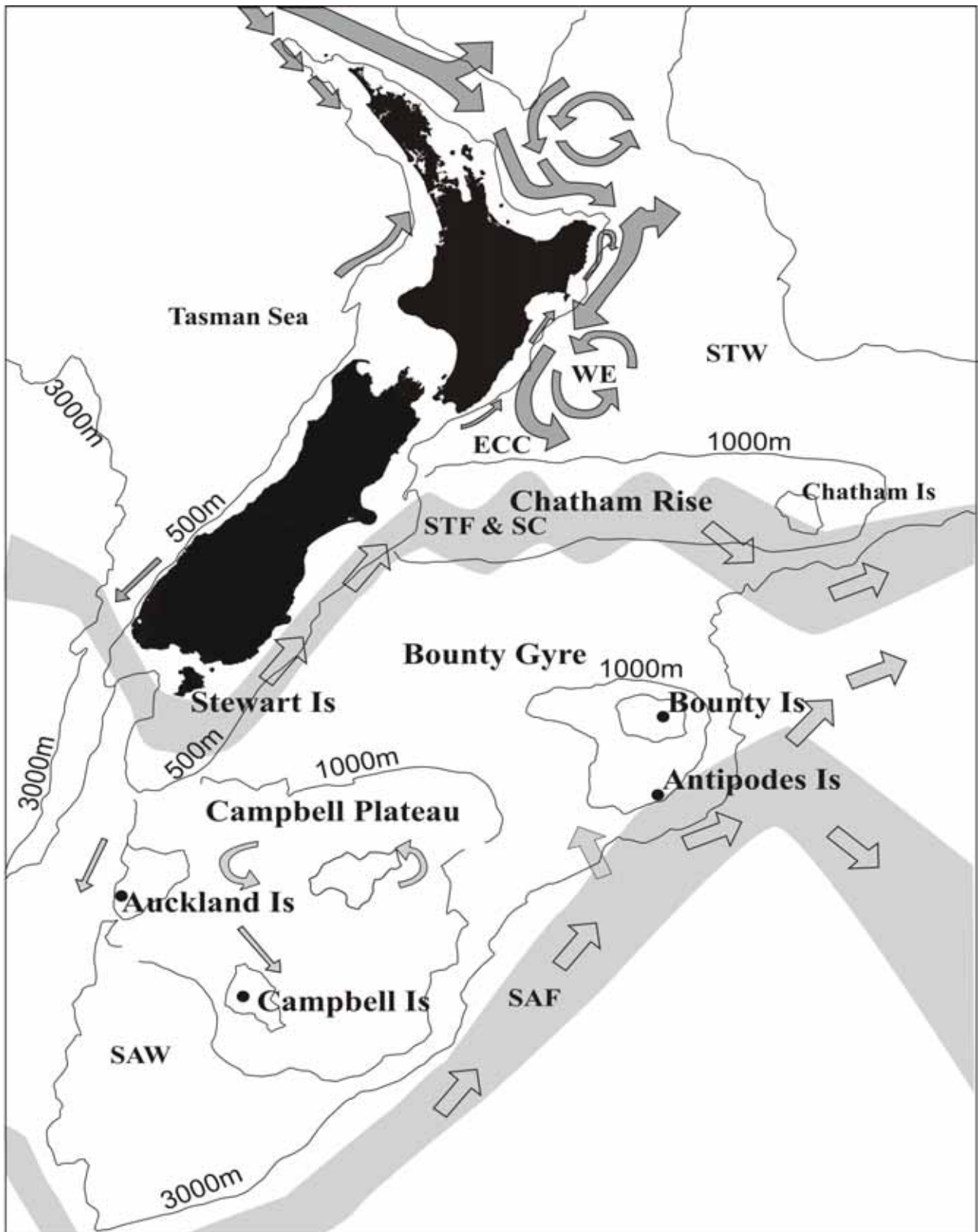


Figure 20. Direction of the marine currents around New Zealand main islands, Chatham Islands and Sub-antarctic islands. Adapted from Goldstien et al. (2009).

lar basis. Other studies also agree with the high male pressure and attribute the number of female morphs to the female’s intention to distract males and avoid the



harassment (Fincke 2004). That could well explain the extreme case with so many *X. tuanui* female forms on the Chatham Island. However, more behavioural investigations are needed as underwater oviposition, for example, is frequently found in the closely allied *X. zealandica* (Rowe 1987).

Survival and abundance

Patterns in survival for *X. tuanui* are consistent with the hypothesis that the harsh environmental conditions impose a strong selective pressure on Chatham Island odonates. The estimates of survival for males and females were 0.75 and 0.50 (or 0.72 if all observations are combined) and are among the lowest observed in odonatological studies. For example, CJS estimates of survival for *Ischnura elegans* (Vander Linden, 1820) in Switzerland were 0.81 and 0.58 for males and females, respectively (Anholt et al. 2001). In this same study, *Coenagrion puella* (male and female combined) were estimated to have survived at a rate of 0.86 per day. Cordero (1992) reports survival rates for *Ischnura graellsii* (Rambur, 1842) ranging between 0.80-0.81 for males and 0.73-0.84 for females. In a comparative research between 12 Zygoptera species Sánchez-Herrera & Realpe (2010) report upon two species only that show lower values: *Calopteryx xanthostoma* (Charpentier, 1840) (0.66) and *Argia vivida* Hagen in Selys, 1865 (0.72). However, *A. vivida's* survival is almost identical with our estimates and the value of 0.66 for *C. xanthostoma* was obtained for males, while females in the same study (Cordero 1989) had greater survival rate of 0.89. Thus, *X. tuanui*, which inhabit an island with highly variable weather, exhibit substantially lower daily survival than what has been measured for odonates in continental systems at temperate latitudes.

Despite their low survival, *X. tuanui* are likely quite abundant in the Chatham Islands. The total population size for both Chatham and Pitt Islands is estimated to be about 6.0 million individuals. This number should be considered an upper estimate for a number of reasons. For example, the spatial analysis in GIS did not consider some important environmental parameters, like wind direction, vegetation



density, stream depth and submerged vegetation—all of which likely affect local abundance, based on behavioural observation. The estimate also lacks other important habitats (e.g., lentic water bodies) that may contribute to the total population size. At this stage, it should be considered an order-of-magnitude approximation of the population size that both islands may harbour. Only through further and more systematic sampling of available habitats can a more accurate estimate be obtained.

Conclusions

Dragonflies living on the Chatham Islands experience extreme environmental conditions in terms of overall low annual temperatures, strong constant wind and high acidification of their larvae biotopes. The potentially short reproductive period, in combination with the harsh climatic situation, could explain the morphological similarity among the Chatham Island and New Zealand main island air-borne insects such as dragonflies, since they have evolved in isolation for 1.8-2.4 million years. Thus the Nolan et al. (2007) results are very interesting and deserve special attention. The two haplotypes that Nolan et al. (2007) have established for genus *Xanthocnemis* on the Chatham Island suggest the occurrence of two species *X. tuanuii* and *X. zealandica*. Two possible alternative scenarios are considered here: 1) secondary dispersal from New Zealand South Island of *X. zealandica* that settled on the Chatham Island after *X. tuanuii* has already completed its lineage sorting, and 2) sympatric speciation on the Chatham Island. The dispersal hypothesis is not to be excluded given the molecular evidence for dispersal rather than vicariance of the Chatham Island flightless insects (Trewick 2000). Dragonflies have been found on the ocean surface (Andersen 1924) or among the “aerial plankton” together with weaker flyers (Holzapfel & Harrell 1968). Yoshimoto et al. (1962) sampled 15 Odonata species with some encountered more than 200 km from land. Species could take advantage of the oceanography of the region and use as resting places floating wood drifting along the subtropical front (fig. 20). However, it would take between 30 to 50 days to



reach the Chatham Island using currents (Chiswell 2009), which makes successful dispersal unlikely even for some marine planktonic stages (Goldstien et al. 2009). Thus if dispersal is accepted as the mode for colonisation of the Chatham Island it must have happened on a direct, wind assisted flight from the South Island, perhaps with possible occasional pauses on drifting materials. The key point is that dispersal should happen after sufficiently long isolation between the Chatham and South Island populations which would result in the establishment of a new species – *X. tuanuii*. Also, it is unclear why dispersal from the South Island towards the Chatham Islands does not happen at present, as morphological studies on adults revealed only individuals with typical of *X. tuanuii* features. Perhaps the greater isolation by distance of the Chatham Island from the source population is a strong limiting factor. McCauley (2006)'s results show a negative correlation between the distance from the source population and number of dragonflies arriving and recruiting into artificially established ponds. In that experiment the water-filled tanks were placed just 1,200 m at a maximum distance from the main genetic pool and they had various level of connectivity between each other.

The situation with Chatham Island (as well as all Pacific islands in general) is much more complicated – hundreds of kilometres from the source population with no freshwater connectivity between. The two haplotypes established for the Chatham Island could also be explained by a hypothetical situation where Nolan et al. (2007) had sampled a site where a new invader from the South Island had just laid eggs, but the *X. zealandica* population failed to establish on the island. Indeed their sampling location at Point Gap is on the western coast of the island and is a potential perching point for the new invaders. However, the likelihood of such scenario is as low as 1:6,000,000, which is the total estimated population size, but does not have to be excluded completely.

The second hypothesis, that both species evolved on the island in sympatry, is considered to be even more unlikely as it assumes that the split of both species could occur on a small island with limited isolation barriers and within a harsh environment. It is, perhaps, easier for reproductive isolation to take place among the ter-



restrial species rather than air-borne taxa. The former have more opportunities to cope with severe environment (hiding among leaf litter, under tree bark or stones), while the later possibly find it much more difficult to overcome those obstacles. The Chatham Island coleopteran fauna is a striking example – 90% of the endemic beetles are in fact flightless (Emberson 1995).

Both hypotheses given above purport that within a harsh environment there has been an intensive period of evolution. However, this is very improbable especially if we accept the short reproduction time for the species living on the Chatham Islands. A third scenario is suggested here based on the morphological analysis only and following the preliminary molecular data reported on larvae by Nolan et al. (2007). Morphologically the Chatham Island *Xanthocnemis* sp. are not significantly different from their South and Stewart Islands counterparts. In most cases the deviations may be explained by the environmental influences (see Discussion). Perhaps, there is a speciation in action and the population on the Chatham Island is beginning to become separate from the South Island (inferred by the great morphological variations in colour morphs and larger size) but has not completed lineage sorting yet: Chatham Island and New Zealand *Xanthocnemis* spp. may be within the so called “Grey Zone” (De Quiroz 2007). This zone is hypothesised as occurring in lineage separation and divergence when the daughter lineages become more and more different from one another: phenetically distinguishable, diagnosable, reciprocally monophyletic, reproductively incompatible, ecologically distinct, and so forth. De Quiroz also suggests that species must be considered as separated even if they do not necessarily acquire all the above mentioned characteristics. They only have to be evolving separately from other lineages, which is what should be investigated for Chatham Island *Xanthocnemis* sp. Its true taxonomic position must therefore be resolved after additional molecular research is performed on the adults.

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