

1 **Predicting biomass of resident kōkopu (*Galaxias*) populations using local habitat**

2 **composition**

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13 **Abstract**

14 With the global decline of freshwater fishes, quantifying the body size-specific
15 habitat use of vulnerable species is crucial for accurately evaluating population health,
16 identifying the effects of anthropogenic stressors, and directing effective habitat
17 restoration. Populations of New Zealand’s endemic kōkopu species (*Galaxias fasciatus*, *G.*
18 *argenteus*, and *G. postvectis*) have declined substantially over the last century in response
19 to anthropogenic stressors, including habitat loss and fragmentation, invasive species, and
20 over-exploitation. Despite well-understood habitat associations, key within-habitat features
21 driving the reach-scale biomass of small and large kōkopu remain unclear. Here, we
22 investigated whether the total biomass of small (≤ 90 mm) and large (> 90 mm) kōkopu was
23 associated with total pool area, average pool depth, total bank cover, average substrate
24 size, and average forest canopy cover across fifty-seven 50 m reaches. These features were
25 selected because generally pool habitats are productive feeding areas, bank cover and
26 substrate interstices are important refuges, and forest cover provides greater food
27 availability. Because kōkopu are nocturnal, populations were sampled with removal at night
28 using headlamps and hand-nets until reaches were visually depleted. Using Akaike’s
29 information criterion, it was found that increases in large kōkopu biomass were most
30 parsimoniously explained by greater pool area and bank cover, whereas increases in small
31 kōkopu biomass were best explained by low bank cover and greater average forest cover.
32 This study demonstrated the importance of considering the ontogenetic shift in species’
33 habitat use and provided an effective modelling approach for quantifying the size-specific
34 habitat use of these stream-dwelling fish.

35 **Introduction**

36 Given the widespread decline of freshwater fishes [1], it is crucial to quantify which
37 habitats are used during all stages of a species' life cycle so that population health can be
38 accurately evaluated, effects of anthropogenic stressors can be tested, and successful
39 rehabilitation measures implemented [2, 3]. Anthropogenic stressors such as pollution,
40 habitat fragmentation and degradation, introduced species, river regulation, and over-
41 exploitation have contributed to a substantial decline in riverine fish populations over the last
42 century [4, 5]. Unfortunately, many statistical models used for studying the effects of
43 anthropogenic stressors on populations are inaccurate due to being calibrated using only a
44 fraction of the habitats used by a species [6]. Without accurate models relating body size and
45 specific habitats, population assessments may be biased, which could lead to ineffective
46 management decisions and unsuccessful, wasteful, or even harmful restoration efforts by
47 excluding important microhabitats such as spawning sites or nursery grounds [7, 8].

48 Influential habitat variables that often determine the habitat selection of stream-
49 dwelling fish include water velocity, in-stream refuges, and overhanging vegetation [9-11].
50 Pools are often preferentially used microhabitats for freshwater fish because they have slower
51 water velocities, which typically reduce an individual's energetic expenditure [12, 13] while
52 improving feeding efficiency [14, 15]. In-stream cover, such as undercut banks, root-wads,
53 debris dams, and interstices between large substratum are important refuges that many fish
54 rely on to minimise the risk of predation and the impacts of physical disturbances [16, 17].
55 Additionally, overhanging vegetation, such as riparian vegetation or forest canopy cover, is
56 linked to a stream's primary productivity and plays a crucial role in providing terrestrial
57 subsidies, in-stream cover, and hydrological stability [18, 19]. Therefore, these habitat
58 features are likely influential determinants of habitat selection during at least one stage of the
59 lifecycle of stream-dwelling fishes.

60 The importance of specific habitat features on habitat selection is often strongly
61 determined by body size [20]. In freshwater fishes, variation in size-related habitat selection
62 is typically due to individual selection of microhabitats that maximise energy gain and
63 minimise energy expenditure or increase survival [21-23]. Because microhabitat selection is
64 strongly linked to individual fitness, species may rely on several distinct microhabitats to
65 support different size-classes [23, 24]. For species where different size-classes inhabit the
66 same local environment, it is vital that restoration efforts incorporate potential ontogenetic
67 shifts in size-specific microhabitat requirements to account for all size-classes in an
68 ecosystem. This is especially important for species that exhibit intraspecific or intra-family
69 competitive hierarchies, because inferior individuals may avoid preferred habitats when
70 dominant congeners are present [25]. Social competitive hierarchies in freshwater fish often
71 follow a size-related structure; large dominant individuals monopolise key feeding habitats
72 and smaller individuals are displaced to less advantageous habitats [26, 27]. Therefore,
73 understanding how abiotic and biotic influences affect the habitat use of distinct size-classes
74 is essential to obtain a robust evaluation of population habitat use.

75 New Zealand's endemic banded kōkopu (*Galaxias fasciatus*), giant kōkopu (*G.*
76 *argenteus*), and shortjaw kōkopu (*G. postvectis*), hereafter collectively referred to as
77 'kōkopu', are diadromous fishes that inhabit the same stream environments during all but
78 their larval life stage. Over the last century, kōkopu have undergone considerable declines in
79 response to a combination of habitat loss, migratory barriers, introduced species, and fishing
80 pressure [28-30]. The loss and degradation of adult habitats through activities including
81 drainage schemes, land-use change, and deforestation are thought to be the biggest drivers of
82 decline in kōkopu [29, 31]. Migratory barriers inhibit upstream dispersal to compatible
83 habitats [32, 33] and introduced species like trout alter kōkopu habitat selection through
84 predation and competitive exclusion [34, 35]. Post-larval kōkopu are also harvested in the

85 culturally, recreationally, and commercially important whitebait fishery [36]. Despite
86 population declines, it is unknown how these anthropogenic stressors specifically alter
87 kōkopu populations due to the lack of accurate size-specific habitat models.

88 Although size-specific habitat models have not been developed for kōkopu, there is a
89 thorough understanding of general habitat preferences [37]. Greater kōkopu densities are
90 often associated with the availability of slow-flowing pools because kōkopu are
91 opportunistic, mostly nocturnal predators, that rely on the transport of aquatic and terrestrial
92 invertebrates into pools from fast-flowing upstream habitats [29, 38]. Banded and shortjaw
93 kōkopu are forest specialists, rarely inhabiting streams without forest canopies, but giant
94 kōkopu also inhabit estuaries, swamps, or ponds [37, 39]. Each species depends on refuge
95 areas for secure diurnal resting, predator escapement, and shelter from flood events [40].
96 Despite having slightly different habitat preferences, the kōkopu species commonly co-occur
97 and share similar environmental requirements (i.e., diet and habitat use), which likely
98 indicates that each species should be influenced similarly by changes to habitat composition
99 from anthropogenic stressors within stream environments.

100 Even though juvenile and adult kōkopu occupy the same local environments,
101 individual microhabitat selection is strongly determined by the presence of larger
102 conspecifics or congeners [41]. For example, small giant kōkopu minimise agonistic
103 interactions with larger dominant conspecifics that control large pools at night by feeding
104 during the day or by occupying alternative microhabitats at night [42]. Similarly, large
105 banded kōkopu prefer deep, slow-flowing pools, with coarse substratum, whereas smaller
106 individuals are likely displaced into shallow pools with faster water velocities and finer
107 substratum [43]. Although size-related kōkopu microhabitat segregation [27, 44, 45] and the
108 influence of habitat composition on total kōkopu biomass [11, 25] are understood, how
109 within-habitat characteristics influence the reach-scale biomass of small and large kōkopu

110 separately is unknown. Such information would provide a more comprehensive and accurate
111 description of kōkopu habitat requirements that could be used to improve habitat restoration
112 efforts. Additionally, by understanding how small and large kōkopu are influenced by local
113 environments, while all other influential environmental variables are being controlled for, a
114 standardised prediction of likely kōkopu biomass based solely on local habitat characteristics
115 can be obtained. These standardised estimates will allow the isolation and accurate testing of
116 how individual environmental manipulations including dispersal barriers, introduced
117 predators, fishing pressure, or habitat restoration efforts affect kōkopu populations by
118 removing habitat-related biases.

119 To examine how kōkopu size-classes respond to habitat composition, all three kōkopu
120 species were studied as one overall ‘population’ because body size is likely the key driver of
121 habitat use, they commonly co-occur, have similar habitat requirements, and abide by intra-
122 family competitive group behaviours [27, 46]. These factors likely mean that one species’
123 position in a stream could be used by either of the other species if it was vacant. A size-class
124 break-point of 90 mm (total length) was used to examine how small and large kōkopu
125 respond to habitat composition. This break-point was selected because banded kōkopu and
126 giant kōkopu are approximately one year old at this size and begin to compete for territory
127 when >90 mm [47-49]. Equivalent studies have not been completed with shortjaw kōkopu,
128 but they were pooled into the same size-class groups for consistency. The similar ecological
129 and physiological characteristics between kōkopu species strongly suggest that the compiled
130 grouping of species will allow an accurate investigation of size-related habitat selection
131 without species-specific biases.

132 We aimed to identify habitat features that influence the biomass of small and large
133 kōkopu. Specifically, we used Akaike’s Information Criterion (AIC), an information theoretic
134 approach [50], to evaluate a candidate set of *a priori* models to explain variation in small and

135 large kōkopu biomass using local habitat features. To achieve this objective, kōkopu
136 populations were surveyed across physically diverse stream reaches. We predicted that: (1)
137 large kōkopu biomass would increase with pool area and depth, whereas small kōkopu
138 biomass would decrease in such habitats, putatively due to larger fish competitively
139 excluding smaller individuals within these key feeding areas; (2) large and small kōkopu
140 biomass would increase with increasing bank cover and substrate size due to both providing
141 refuges to all size-classes; and (3) both large and small kōkopu biomass would increase with
142 forest canopy cover due to it likely providing greater food availability.

143 **Methods**

144 *Study Sites*

145 To investigate which habitat features are most strongly associated with reach-scale
146 kōkopu biomass, three 50 m reaches were sampled within each of 19 streams on the West
147 Coast of New Zealand's South Island during May and June 2021. Local topographic maps,
148 site visits, and databases, such as Freshwater Ecosystems of New Zealand (FENZ; [51]) and
149 the New Zealand Freshwater Fish Database (NZFFD; [52]), were used to select streams that
150 contained kōkopu and that had no fish passage barriers or trout presence. All streams were
151 open to whitebait fishing because unfished streams were limited. Physically diverse streams
152 that included a wide range of habitat compositions were selected to provide a robust
153 understanding of how individual habitat variables influenced kōkopu biomass. Sampling took
154 place within two months to minimise seasonal differences in kōkopu biomass.

155

156 *Habitat survey*

157 Study reaches began and ended at riffles, which acted as minor fish barriers between
158 reaches, were located in areas with minimal surface turbulence or natural visual-obstruction
159 deposits (i.e., foam or fine debris collections), and were no deeper than 1.5 m. Habitat

160 surveys, completed during daylight hours, involved measuring the area and average depth of
161 pools, availability of in-stream bank cover, average substrate size, and percentage cover of
162 forest canopy within each reach. Forest cover was measured at approximately eight locations
163 within each reach using a spherical crown densiometer [53] while standing in the middle of
164 the waterway and facing upstream. In-stream bank cover was recorded by measuring the
165 perimeter of root wads, undercut banks, or debris dams accessible to fish. Pool area was
166 calculated using:

$$167 \quad PA = (W/2) \times (L/2) \times \pi \quad (\text{Eq. 1.})$$

168 where PA is pool area (m^2), W is the maximum width of the pool (m), and L is the maximum
169 length of the pool (m). Average pool depth was calculated from ten depth measurements
170 along the W axis. The average substrate size within each reach was calculated from
171 approximately 60 stones randomly selected using a Wolman's walk [54].

172

173 ***Kōkopu biomass survey***

174 The three 50 m reaches within each stream were sampled starting >1 h after sunset
175 (using spotlighting) when kōkopu are active. Sampling consisted of counting kōkopu using a
176 high-powered spotlight to scan the reach for fish in slow-flowing habitats [55]. This method
177 has been used effectively for sampling kōkopu within wadeable streams at night [34, 56].
178 Alternative fish sampling methods such as electrofishing and trapping are generally less
179 effective for surveying kōkopu because they sink when stunned, occupy deep bank cover
180 during the day, and may not encounter traps due to having high pool fidelity at night [57-59].
181 The 1 h delay after sunset ensured that resident kōkopu had left their daytime refuges and
182 moved into nocturnal foraging areas where they could be seen and captured. When spotted,
183 kōkopu generally remained stationary and were caught using hand nets. All captured fish
184 were placed into buckets of aerated stream water. When kōkopu were seen but not caught, the

185 estimated length and species of the individual were recorded and noted as a ‘miss’. Reaches
186 were sampled using successive depletion passes until fish were no longer observed. This
187 required up to five passes and took around 1.5 h per reach. Captured kōkopu were
188 anaesthetised in 20 mg/L of AQUI-S water-dispersible liquid anaesthetic to facilitate
189 handling. The total length of each fish was measured on a wet measuring board (± 1 mm)
190 before being weighed (± 0.01 g). After measurements were taken, fish were placed in buckets
191 of fresh stream water to recover, and then returned to their area of capture. All procedures
192 were approved by the University of Canterbury Animal Ethics Committee (permit number
193 2020/06R).

194

195 ***Data analysis***

196 Prior to analyses, large and small kōkopu biomass responses were square root
197 transformed to meet assumptions of normality, and outliers (two large kōkopu responses and
198 one small kōkopu response) were identified and removed using interquartile range criterion.
199 Biomass measurements were used as a response instead of counts because kōkopu body mass
200 varies substantially between individuals and is associated with available resources, whereas
201 the association between fish counts and resource availability is also determined by
202 competitive interactions [25]. Variance inflation factors (VIF) were calculated to ensure that
203 there was no collinearity between predictors (i.e., $VIF \leq 4$; [60]). Because all VIF values
204 were low ($VIF < 2.0$) we proceeded with model selection.

205 To assess how local habitat composition influenced kōkopu biomass, a set of
206 ecologically realistic *a priori* linear mixed-effects models, which included all combinations
207 of the five habitat variables, was used to explain the biomass of each kōkopu size-class.
208 Ecologically realistic interactions between habitat features were initially included, but later
209 removed due to poor data spread creating unreliable results. Linear mixed-effects models

210 were constructed using the ‘lme’ function (Package ‘nlme’; [61]) in R version 4.1.1 [62] and
211 included a random factor for stream so that each of the three reaches nested within a stream
212 could be independently used to examine how habitat composition influenced kōkopu
213 biomass. By focusing on the reach-scale, more accurate and informative localised habitat-
214 biomass relationships could be obtained.

215 An information theoretic approach, using Akaike’s information criterion corrected for
216 small sample size (AIC_c), was used to determine which candidate models explained variation
217 in large and small kōkopu biomass most parsimoniously [50]. Each model’s AIC_c was
218 subtracted from the lowest AIC_c to determine its ΔAIC_c [50]. Parsimonious models had
219 ΔAIC_c values < 2 [63]. Conditional coefficient of determination (R^2_c ; proportion of variance
220 explained by fixed and random effects) values were calculated for each parsimonious model
221 to evaluate goodness-of-fit because AIC_c only ranks models relative to each other [64, 65].
222 The Akaike weight and R^2_c of parsimonious models were compared to select the most
223 suitable model for explaining large and small kōkopu biomass.

224 Partial dependence plots, which show the independent effect of a single variable on the
225 response by accounting for the average effects of all other variables in a model [66], were
226 used to visually examine the independent effect of each habitat feature on the total biomass of
227 large and small kōkopu. Using the ‘effects’ package [67], partial dependence plots were
228 developed by extracting the independent effects of each variable within a linear mixed-effects
229 model that included all five habitat features and a random factor for stream on the biomass of
230 each size-class.

231

232 **Results**

233 Large kōkopu biomass was explained parsimoniously (i.e., a $\Delta AIC_c < 2$) by two
234 models (Table 1). Predictors in the first model (1L) were total bank cover and pool area,

235 while the second model (2L) also included total bank cover and pool area, but added average
236 substrate size. Large kōkopu biomass was positively correlated with total pool area (R^2_c
237 =0.19, $F_{1,53}=12.45$, $P<0.001$; Fig. 1a), total bank cover ($R^2_c=0.26$, $F_{1,53}=18.75$, $P<0.001$; Fig.
238 1c), and average substrate size ($R^2_c=0.11$, $F_{1,53}=6.79$, $P=0.012$; Fig. 1d). However, there was
239 no correlation between large kōkopu biomass and average pool depth ($R^2_c <0.01$, $F_{1,53}=0.02$,
240 $P=0.883$; Fig. 1b) or forest cover ($R^2_c <0.1$, $F_{1,53}=0.45$, $P=0.505$; Fig. 1e). Despite having
241 fewer explanatory variables, model 1L explained just 4% less variation than model 2L ($R^2_c =$
242 0.51 and 0.55, respectively; Table 1). Model 1L also better accounted for variation in large
243 kōkopu biomass, as indicated by the Akaike weights of 0.21 and 0.16, respectively. This
244 suggested that model 1L was the most suitable for predicting large kōkopu biomass. Table 2
245 details the summary statistics for model 1L.

246 In contrast to large kōkopu biomass, small kōkopu biomass was negatively correlated
247 with bank cover ($R^2_c=0.33$, $F_{1,54}=27.05$, $P<0.001$; Fig. 1h) and substrate size ($R^2_c=0.11$,
248 $F_{1,54}=6.33$, $P=0.012$; Fig. 1d), but positively correlated with forest cover ($R^2_c=0.25$,
249 $F_{1,54}=18.64$, $P<0.001$; Fig. 1j). Additionally, small kōkopu biomass was not correlated with
250 pool area ($R^2_c=0.03$, $F_{1,54}=1.78$, $P=0.188$; Fig. 1f) or pool depth ($R^2_c=0.01$, $F_{1,54}=0.78$,
251 $P=0.382$; Fig. 1g). Four models explained small kōkopu biomass parsimoniously (Table 1).
252 The first model (1S), which included forest cover and bank cover, explained 3% less
253 variation than the most explanatory model (3S), which also included pool area ($R^2_c=0.58$ and
254 0.61, respectively). However, model 1S was 9% more likely to explain variation in small
255 kōkopu biomass most parsimoniously than the second model (2S), which also included
256 average substrate size (Akaike weights = 0.20 and 0.11, respectively). This suggested that
257 model 1S was the most suitable for predicting small kōkopu biomass. Table 2 details the
258 summary statistics for model 1S.

259 **Table 1. Top linear mixed-effects models ($\Delta AIC_c < 2$) that explain variation in the total**
 260 **biomass of large and small kōkopu based on Akaike’s information criterion (AIC).**

Response	Model	Fixed effects	AIC_c	ΔAIC_c	w	R^2_c
Large kōkopu						
$\sqrt{\text{Large kōkopu biomass}}$	1L	BC + PA	346.7	0.00	0.20	0.51
	2L	BC + PA + SS	347.1	0.46	0.16	0.55
Small kōkopu						
$\sqrt{\text{Small kōkopu biomass}}$	1S	FC + BC	203.4	0.00	0.20	0.58
	2S	FC + BC + SS	204.6	1.20	0.11	0.58
	3S	FC + BC + PA	205.1	1.78	0.08	0.61
	4S	FC	205.3	1.96	0.07	0.5

261 AIC_c represents AIC values corrected for small sample size, delta AIC_c (ΔAIC_c) is the
 262 difference in AIC_c score between the highest ranked model and the candidate model, the
 263 Akaike weight (w) is the probability that a particular model is the most parsimonious model
 264 among the candidate models, and R^2_c is the conditional coefficient of determination. ‘BC’ is
 265 total bank cover (m), ‘PA’ is total pool area (m²), ‘SS’ is average substrate size (cm), and
 266 ‘FC’ is mean forest cover (%). Models are listed from lowest to highest AIC_c score within
 267 each size-class. Bolded models were selected as the most suitable for predicting biomass
 268 within each size-class.

269 **Table 2. Summary results of the fixed effects included in the linear mixed-effects models**
 270 **that most parsimoniously predict the total biomass of large and small kōkopu as**
 271 **identified in Table 1.**

Model	Fixed effects	Coefficient estimate (\pm SE)	P value
Large kōkopu			
$\sqrt{\text{Large kōkopu biomass}} \sim \text{BC} + \text{PA}$	Intercept	5.016 (\pm 1.986)	0.016
	BC	0.108 (\pm 0.049)	0.036
	PA	0.031 (\pm 0.015)	0.04
Small kōkopu			
$\sqrt{\text{Small kōkopu biomass}} \sim \text{FC} + \text{BC}$	Intercept	3.033 (\pm 0.756)	<0.001
	FC	0.020 (\pm 0.009)	0.041
	BC	-0.026 (\pm 0.012)	0.035

272 ‘BC’ is total bank cover (m), ‘PA’ is total pool area (m²), and ‘FC’ is mean forest cover (%).

273

274 **Fig 1. Relationships between habitat features and kōkopu biomass.** Partial regression
 275 plots showing the independent effect of total pool area (a, f), mean pool depth (b, g), total
 276 bank cover (c, h), mean substrate size (d, i), and mean forest cover (e, j) on large (row 1), and
 277 small kōkopu biomass (row 2). Note that the Y-axis is not linear. Dots represent the total
 278 biomass of giant, banded, and shortjaw kōkopu in the size-class within each 50 m reach.
 279 Lines of best fit are shown where a significant correlation was found ($P < 0.05$) and error
 280 bands show 95% confidence intervals determined from model fits.

281

282 Discussion

283 The quantification of body size with respect to specific habitat use is crucial for
 284 accurately identifying key habitats that support all life stages of a species and directing
 285 beneficial management and restoration efforts [68]. We aimed to identify key habitat features
 286 that influence the biomass of small and large kōkopu, and to create statistical models that can
 287 predict kōkopu biomass based on local habitat features while controlling for other influences.
 288 Our results indicate that small and large kōkopu have distinct habitat requirements, and the
 289 influence of habitat composition on biomass was not consistent between size-classes. By

290 characterising the effects of local habitat composition on the biomass of small and large
291 kōkopu separately, we provide a more comprehensive and accurate description of kōkopu
292 habitat requirements.

293 Total pool area was a key habitat feature for explaining variation in large kōkopu
294 biomass, whereas average pool depth had little influence. This indicates that large kōkopu
295 can use most pool habitats, regardless of depth. Pool habitats are commonly associated with
296 greater biomasses of large stream-dwelling fish like salmonids [69, 70]. Positive correlations
297 between pool area and large fish biomass is expected, because although faster water
298 velocities transport more drifting invertebrates downstream, slower flowing habitats such as
299 pools promote greater feeding success by increasing strike efficiency and prey capture [23].
300 However, species like kōkopu and trout will maximise their net energy gain by occupying
301 slow-flowing pools below fast-flowing reaches [2, 15, 71]. Unlike trout, which are
302 predominantly diurnal visual predators, nocturnal galaxiids rely mainly on mechanical lateral
303 line and olfactory sensory systems that work most effectively in slow-velocities [72, 73].
304 Therefore, similarly to other large stream fish, slow-flowing pools likely support greater large
305 kōkopu biomass because they are profitable foraging areas.

306 Despite pool area being a key habitat requirement for large kōkopu, neither total pool
307 area nor average pool depth influenced small kōkopu biomass. The lack of relationship
308 between small kōkopu and pool habitat was likely caused by the greater biomass of large
309 congeners, which were not restricted by pool depth, competitively displacing smaller
310 individuals [45, 74]. Small kōkopu may also avoid pools because large individuals
311 cannibalise smaller congeners [44, 75]. Similar relationships have been observed in drift-
312 feeding cutthroat trout (*Oncorhynchus clarkii*); large fish occupy deep pools and smaller
313 young-of-the-year inhabit shallower water [76]. However, in the absence of large
314 conspecifics, small trout choose, and grow faster in, large pools over shallower water [26].

315 Although small kōkopu are likely displaced into less profitable foraging areas, they still select
316 habitats with the lowest available velocity [43]. This suggests that slow-flowing pools may be
317 included in the fundamental niche of small kōkopu, but biotic interactions with larger
318 predators result in these areas falling outside of their realised niche.

319 In addition to pool habitat, in-stream refuges and large substratum were important
320 habitat features that were positively associated with large kōkopu biomass. However, unlike
321 their larger congeners, these features were negatively associated with small kōkopu biomass.
322 Despite hypothesising that small kōkopu would also use these features for refuges, our results
323 show that large kōkopu dominate these areas, suggesting they competitively displace smaller
324 individuals from them. Similarly to kōkopu, in-stream cover is thought to be the most
325 important habitat feature influencing juvenile and adult salmonid habitat selection [77].
326 However, most experimental studies that have added wood to streams have found that
327 juvenile and adult salmonids respond positively [78]. It is important to consider that habitat
328 structure can also increase predation risk by providing predator habitat [79]. In addition to
329 large kōkopu, longfin eels (*Anguilla dieffenbachii*) also benefit from greater bank cover
330 availability, which could also lead to small kōkopu avoiding these microhabitats [17].
331 Although there are contrasting accounts of preferred in-stream cover, adult banded kōkopu
332 and giant kōkopu will readily use alternative bank cover when preferred cover is scarce [37].
333 This suggests that compiling various forms of bank cover into one variable is acceptable for
334 kōkopu habitat-biomass modelling. In-stream cover is likely the most influential habitat
335 feature on kōkopu biomass due to the strong conflicting effects on small and large kōkopu
336 biomass.

337 Unlike pool area and in-stream cover, forest cover was not associated with large
338 kōkopu biomass. This was unexpected because forested streams generally provide important
339 terrestrially-derived food subsidies that can support greater fish biomass and contribute up to

340 half the annual energy budget of some drift-feeding species [80, 81]. However, we sampled
341 in autumn when terrestrial subsidies substantially reduce seasonally [81]. Terrestrial
342 invertebrates are an essential food resource for banded kōkopu, making up 75% of their diet
343 by number, and 89% by weight [58]. Importantly, our method of surveying forest canopy
344 cover within reaches using a densitometer may not accurately represent the availability of
345 terrestrial food resources because it measures the canopy immediately over the reach,
346 whereas resources can be sourced from further upstream or from lower-growing riparian
347 vegetation. Overall, forest cover is not locally important in explaining large kōkopu biomass.

348 In contrast to large kōkopu, forest cover was the only habitat feature that was
349 positively associated with small kōkopu biomass. This was somewhat expected because
350 banded kōkopu post-larvae migrate in greater abundances into streams that drain catchments
351 with greater indigenous forest cover [36]. McDowall [82] hypothesised that kōkopu post-
352 larvae may use warmer water temperatures to identify more-forested catchments in contrast
353 to cooler streams that are derived from glaciers and mountainous regions. It is unclear to what
354 extent small kōkopu benefit from terrestrially-derived food subsidies because their small gape
355 size may inhibit the capture of larger terrestrial invertebrates [83]. Additionally, because
356 small kōkopu are displaced competitively from key feeding areas such as pools, smaller fish
357 would have less access to terrestrial invertebrates. However, forested streams can support
358 much greater densities of mayflies, stoneflies, and caddisflies that are more suitable prey for
359 fish with a smaller gape size [84]. The size-specific importance of stream shading could be
360 attributed to smaller kōkopu being more at risk of predation from visually feeding avian
361 predators such as kingfishers (*Todiramphus sanctus*) due to being displaced from daytime
362 refuges. In less shaded shallow streams, small cutthroat trout were more susceptible to visual
363 avian predators than large trout because of predator gape-limitations [85]. Furthermore, shade
364 was particularly important when in-stream cover was limited [85]. This indicates that small

365 kōkopu may occupy reaches with greater forest canopy cover to reduce the likelihood of
366 predation rather than for terrestrial inputs.

367 The absence of mutually benefitting habitat features on small and large kōkopu
368 biomass indicates that there is no key feature that can be used to benefit all of the life stages
369 of kōkopu, and that habitat restoration efforts will need to consider small and large kōkopu
370 habitats concurrently. Because of these conflicts, it is important to identify which habitat
371 compositions provide the greatest benefits to the population of reproductively valuable adults
372 over time [86]. If juvenile habitats are limited or degraded, adult populations may become
373 limited by recruits [87]. However, if an adult population typically has excess recruits and is
374 limited by habitat then the most beneficial management decisions could be to prioritise adult
375 habitats. Often, a balance of adult and juvenile habitat requirements must be incorporated into
376 management restoration to benefit the overall population. For example, gravel augmentation
377 is a key tool used for restoring salmonid spawning and incubation grounds [88]. However, a
378 conflict arose when adult Chinook salmon (*Oncorhynchus tshawytscha*) preferentially
379 spawned in fine gravels where embryo survival was least likely [88]. Therefore, it was
380 suggested that intermediate sized gravels would maximize overall reproductive success
381 across both spawning and incubation life stages. Comparatively, despite being associated
382 with a decrease in small kōkopu biomass, there would likely be greater conservation benefits
383 in adding in-stream refuges into reaches with habitat-limited adult kōkopu populations and
384 excess juveniles, due to adults being reproductively valuable. Further research is required to
385 investigate which balance of juvenile and adult habitats provides the greatest benefits to
386 kōkopu populations.

387 In conclusion, this study demonstrates the importance of examining size-related
388 habitat use when identifying key habitats that support species, and provides a detailed and
389 effective modelling approach for predicting small and large size-classes of stream fish using

390 simple habitat measurements. We showed that large kōkopu biomass was best explained by a
391 combination of total pool area and bank cover availability, whereas small kōkopu biomass
392 was best explained by a combination of total bank cover and average forest cover. With this
393 enhanced understanding of how kōkopu size-classes are influenced by their local
394 environments, we can obtain a standardised prediction of likely kōkopu biomass based on
395 local habitat characteristics. These standardised predictions can be used to isolate and
396 accurately test how anthropogenic stressors affect populations of these declining endemic
397 kōkopu species [86]. Modelling techniques such as those presented in this study will likely be
398 a crucial tool used in conserving freshwater fish species by effectively evaluating population
399 distributions and densities, streamlining habitat restoration efforts, and mitigating
400 anthropogenic stressors [89].

401

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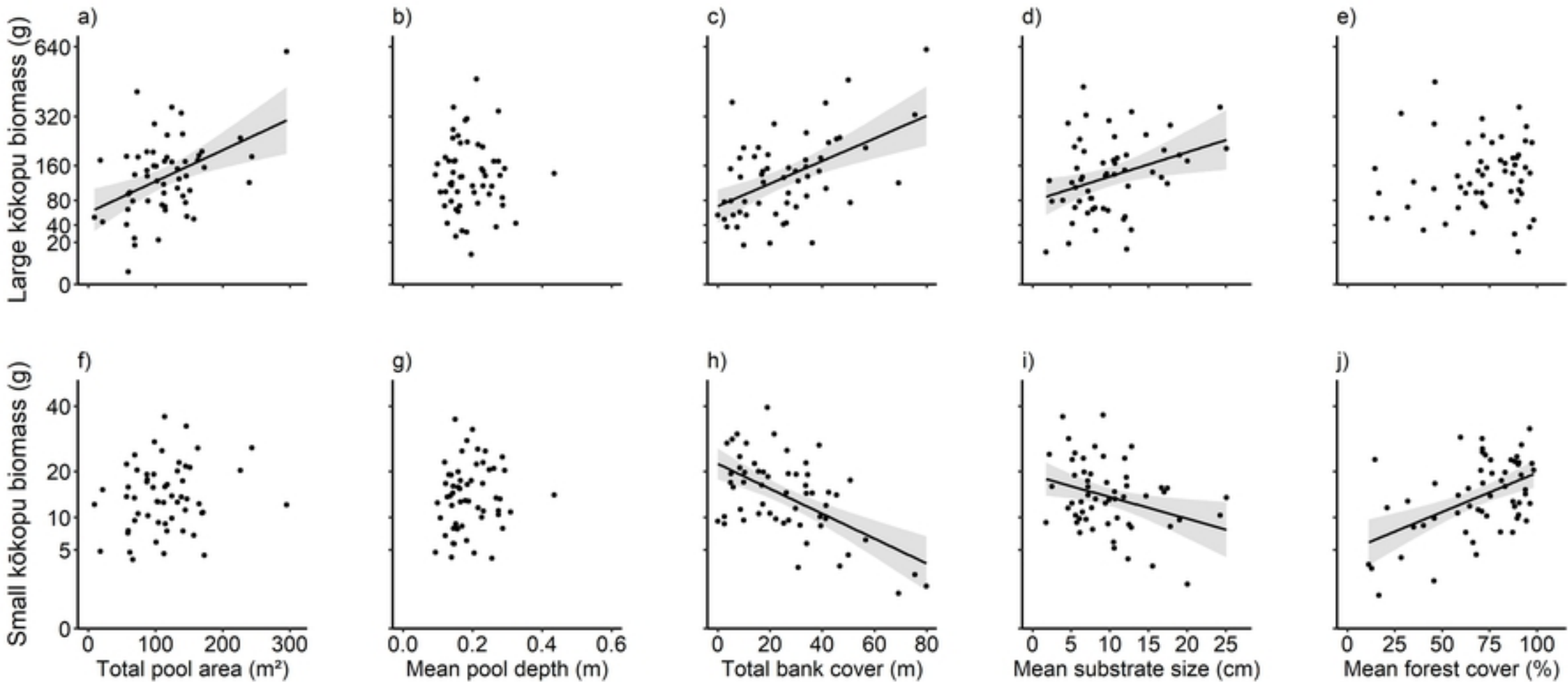


Fig1