1

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

composition

Ben R. J. Crichton[1,*], Michael J.H. Hickford[1], Angus R. McIntosh[2], David R. Schiel[1]

[1]Marine Ecology Research Group, School of Biological Sciences, University of Canterbury, Christchurch, New Zealand

[2]Marine Ecology Research Group, School of Biological Sciences, University of Canterbury, Christchurch, New Zealand

*Corresponding author email: ben.crichton@pg.canterbury.ac.nz

2

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.

3

Introduction

35

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.

4

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 congenerics [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

6

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

7

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

8

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

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 ΔAICc < 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.

12

Table 1. Top linear mixed-effects models ($\Delta AIC_c < 2$) that explain variation in the total 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

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

13

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

272 'BC' is total bank cover (m), 'PA' is total pool area (m^2), 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

14

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].

15

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

Acknowledgements

References

408   1.   Abell R. Conservation biology for the biodiversity crisis: a freshwater follow-up.
409   Conservation Biology. 2002;16(5):1435-1437.
410   2.   Banish NP, Peterson JT, Thurow RF. Physical, biotic, and sampling influences on diel
411   habitat use by stream-dwelling bull trout. North American Journal of Fisheries Management.
412   2008;28(1):176-187.
413   3.   Smialek N, Pander J, Mueller M, van Treeck R, Wolter C, Geist J. Do we know enough
414   to save European riverine fish?—a systematic review on autecological requirements during
415   critical life stages of 10 rheophilic species at risk. Sustainability. 2019;11(18).
416   4.   Dudgeon D, Arthington AH, Gessner MO, Kawabata Z-I, Knowler DJ, Lévêque C, et al.
417   Freshwater biodiversity: importance, threats, status and conservation challenges. Biological
418   reviews of the Cambridge Philosophical Society. 2006;81(2):163-182.

419   5.   Arthington AH, Dulvy NK, Gladstone W, Winfield IJ. Fish conservation in freshwater
420   and marine realms: status, threats and management. Aquatic Conservation: marine and
421   Freshwater Ecosystems. 2016;26(5):838-857.
422   6.   Logez M, Bady P, Pont D. Modelling the habitat requirement of riverine fish species
423   at the European scale: sensitivity to temperature and precipitation and associated
424   uncertainty. Ecology of Freshwater Fish. 2012;21(2):266-282.
425   7.   Van Looy K, Tonkin JD, Floury M, Leigh C, Soininen J, Larsen S, et al. The three Rs of
426   river ecosystem resilience: resources, recruitment, and refugia. River Research and
427   Applications. 2019;35(2):107-120.
428   8.   Oele DL, Gaeta JW, Rypel AL, McIntyre PB. Growth and recruitment dynamics of
429   young-of-year northern pike: implications for habitat conservation and management.
430   Ecology of Freshwater Fish. 2018;28(2):285-301.
431   9.   Inoue M, Nakano S, Nakamura F. Juvenile masu salmon (*Oncorhynchus masou*)
432   abundance and stream habitat relationships in northern Japan. Canadian Journal of
433   Fisheries and Aquatic Sciences. 1997;54:1331-1341.
434   10.   Bonnett ML, Sykes JRE. Habitat preferences of giant kokopu, *Galaxias argenteus*.
435   New Zealand Journal of Marine and Freshwater Research. 2002;36(1):13-24.
436   11.   Akbaripasand A, Closs GP. Effects of food supply and stream physical characteristics
437   on habitat use of a stream-dwelling fish. Ecology of Freshwater Fish. 2018;27(1):270-279.
438   12.   Facey DE, Grossman GD. The relationship between water velocity, energetic costs,
439   and microhabitat use in four North American stream fishes. Hydrobiologia. 1992;239(1):1-6.
440   13.   Pert EJ, Erman DC. Habitat use by adult rainbow trout under moderate artificial
441   fluctuations in flow. Transactions of the American Fisheries Society. 1994;123(6):913-923.
442   14.   Rosenfeld JS, Boss S. Fitness consequences of habitat use for juvenile cutthroat
443   trout: energetic costs and benefits in pools and riffles. Canadian Journal of Fisheries and
444   Aquatic Sciences. 2001;58(3):585-593.
445   15.   Naman SM, Rosenfeld JS, Kiffney PM, Richardson JS. The energetic consequences of
446   habitat structure for forest stream salmonids. Journal of Animal Ecology. 2018;87(5):1383-
447   1394.
448   16.   Skyfield JP, Grossman GD. Microhabitat use, movements and abundance of gilt
449   darters (*Percina evides*) in southern Appalachian (USA) streams. Ecology of Freshwater Fish.
450   2008;17(2):219-230.
451   17.   Baillie BR, Hicks BJ, van den Heuvel MR, Kimberley MO, Hogg ID. The effects of wood
452   on stream habitat and native fish assemblages in New Zealand. Ecology of Freshwater Fish.
453   2013;22(4):553-566.
454   18.   Dolloff CA, Warren MLJ. Fish relationships with large wood in small streams.
455   American Fisheries Society Symposium. 2003;37:179-193.
456   19.   Zalewski M, Lapimska M, Bayley PB. Fish relationships with wood in large rivers.
457   American Fisheries Society Symposium. 2003:1-17.
458   20.   Heggenes J. Habitat selection by brown trout (*Salmo trutta*) and young Atlantic
459   salmon (*S. salar*) in streams: static and dynamic hydraulic modelling. Regulated rivers.
460   1996;12(2-3):155-169.
461   21.   Hill J, Grossman GD. An energetic model of microhabitat use for rainbow trout and
462   rosyside dace. Ecology. 1993;74(3):685-698.
463   22.   Petty JT, Grossman GD. Patch selection by mottled sculpin (Pisces: Cottidae) in a
464   southern Appalachian stream. Freshwater Biology. 1996;35:261-276.

465   23.   Grossman GD, Rincon PA, Farr MD, Ratajczak REJ. A new optimal foraging model
466   predicts habitat use by drift-feeding stream minnows. Ecology of Freshwater Fish.
467   2002;11:2-10.
468   24.   Lapointe NWR, Corkum LD, Mandrak NE. Seasonal and ontogenic shifts in
469   microhabitat selection by fishes in the shallow waters of the detroit river, a large connecting
470   channel. Transactions of the American Fisheries Society. 2011;136(1):155-166.
471   25.   Hansen EA, Closs GP. Long-term growth and movement in relation to food supply
472   and social status in a stream fish. Behavioral Ecology. 2009;20(3):616-623.
473   26.   Rosenfeld J. Assessing the habitat requirements of stream fishes: an overview and
474   evaluation of different approaches. Transactions of the American Fisheries Society.
475   2003;132:953-968.
476   27.   Akbaripasand A, Ramezani J, Lokman PM, Closs GP. Does social status within a
477   dominance hierarchy mediate individual growth, residency and relocation? Oecologia.
478   2014;176(3):771-779.
479   28.   Swales S, West DW. Distribution, abundance and conservation status of native fish in
480   some Waikato streams in the North Island of New Zealand. Journal of the Royal Society of
481   New Zealand. 1991;21(4):281-296.
482   29.   Bonnett ML, McDowall RM, Sykes JRE. Critical habitats for the conservation of giant
483   kokopu, *Galaxias argenteus* (Gmelin, 1789). Science for Conservation. 2002;206:50.
484   30.   Jowett IG, Hayes JW, Deans N, Eldon GA. Comparison of fish communities and
485   abundance in unmodified streams of Kahurangi National Park with other areas of New
486   Zealand. New Zealand Journal of Marine and Freshwater Research. 1998;32(2):307-322.
487   31.   Rowe D, Hicks M, Richardson J. Reduced abundance of banded kokopu (*Galaxias*
488   *fasciatus*) and other native fish in turbid rivers of the North Island of New Zealand. New
489   Zealand Journal of Marine and Freshwater Research. 2000;34(3):547-558.
490   32.   Eikaas HSM, A. Habitat loss through disruption of constrained dispersal networks.
491   Ecological Applications. 2006;16(3):987-998.
492   33.   David BO, Hamer MP. Remediation of a perched stream culvert with ropes improves
493   fish passage. Marine and Freshwater Research. 2012;63(5): 440-449.
494   34.   David BO, Closs GP, Arbuckle CJ. Distribution of fish in tributaries of the lower
495   Taieri/Waipori rivers, South Island, New Zealand. New Zealand Journal of Marine and
496   Freshwater Research. 2002;36(4):797-808.
497   35.   Goodman J. The ecology and conservation of shortjaw kokopu (*Galaxias postvectis*)
498   in Nelson and Marlborough. MSc. thesis, University of Canterbury, Christchurch, New
499   Zealand; 2002.
500   36.   Yungnickel MR, Hickford MJH, Schiel DR. Spatio-temporal variation in species
501   composition of New Zealand's whitebait fishery. New Zealand Journal of Marine and
502   Freshwater Research. 2020;54(4):679-694.
503   37.   Baker CF, Smith JP. Habitat use by banded kokopu (*Galaxias fasciatus*) and giant
504   kokopu (*G. argenteus*) co-occurring in streams draining the Hakarimata Range, New
505   Zealand. New Zealand Journal of Marine and Freshwater Research. 2007;41(1):25-33.
506   38.   McDowall RM, Main MR, West DW, Lyon GL. Terrestrial and benthic foods in the diet
507   of the shortjawed kokopu, *Galaxias postvectis* Clarke (Teleostei: Galaxiidae). New Zealand
508   Journal of Marine and Freshwater Research. 1996;30(2):257-269.
509   39.   McDowall RM. Indigenous vegetation type and the distribution of shortjawed
510   kokopu, *Galaxias postvectis* (Teleostei: Galaxiidae), in New Zealand. New Zealand Journal of
511   Zoology. 1997;24(3):243-255.

512   40.   Rowe DK, Smith J. Use of in-stream cover types by adult banded kokopu (*Galaxias*
513   *fasciatus*) in first-order North Island, New Zealand, streams. New Zealand Journal of Marine
514   and Freshwater Research. 2003;37(3):541-552.
515   41.   Chadderton WL, Allibone RM. Habitat use and longitudinal distribution patterns of
516   native fish from a near pristine Stewart Island, New Zealand, stream. New Zealand Journal
517   of Marine and Freshwater Research. 2000;34(3):487-499.
518   42.   Hansen EA, Closs GP. Diel activity and home range size in relation to food supply in a
519   drift-feeding stream fish. Behavioral Ecology. 2005;16(3):640-648.
520   43.   Akbaripasand A, Nichol EC, Lokman PM, Closs GP. Microhabitat use of a native New
521   Zealand galaxiid fish, *Galaxias fasciatus*. New Zealand Journal of Marine and Freshwater
522   Research. 2011;45(1):135-144.
523   44.   Whitehead A. Ontogenetic shift in nocturnal microhabitat selection by giant kokopu
524   in a New Zealand stream. Journal of Fish Biology. 2002;61(6):1373-1385.
525   45.   David BO, Closs GP, Crow SK, Hansen EA. Is diel activity determined by social rank in
526   a drift-feeding stream fish dominance hierarchy? Animal Behaviour. 2007;74(2):259-263.
527   46.   Jowett IG, Richardson J. Fish communities in New Zealand rivers and their
528   relationship to environmental variables. New Zealand Journal of Marine and Freshwater
529   Research. 2003;37(2):347-366.
530   47.   Hopkins CL. Age-related growth characteristics of *Galaxias fasciatus* (Salmoniformes:
531   Galaxiidae). New Zealand Journal of Marine and Freshwater Research. 1979;13(1):39-46.
532   48.   McCullough CD. Abundance, behaviour, and habitat requirements of the banded
533   kokopu *Galaxias fasciatus* Gray (Pisces: Galaxiidae). MSc. thesis, University of Waikato;
534   1998.
535   49.   Jellyman DJ. Observations on the biology of the giant kokopu, *Galaxias argenteus*
536   (Gmelin 1789). Mauri Ora. 1979;7:53-61.
537   50.   Burnham KP, Anderson DR. Model selection and multimodel inference: a practical
538   information-theoretic approach. 2nd ed. New York: Springer; 2002.
539   51.   Leathwick JR, West D, Chadderton L, Gerbeaux P, Kelly D, Robertson H, et al.
540   Freshwater Ecosystems of New Zealand (FENZ) geodatabase user guide. 2010.
541   52.   National Institute of Water and Atmospheric Research. New Zealand Freshwater Fish
542   Database 2021. Available from: https://nzffdms.niwa.co.nz/.
543   53.   Lemmon PE. A new instrument for measuring forest overstory density. Journal of
544   Forestry. 1957;55(9):667-668.
545   54.   Mosley MP. A procedure for characterising river channels. Ministry of Works and
546   Development Water and Soil Miscellaneous Publication 32. 1982:68 p.
547   55.   Joy M, David B, Lake MD. New Zealand freshwater fish sampling protocols: part 1,
548   wadeable rivers & streams. The Ecology Group, Massey University. 2013.
549   56.   David BO, Closs GP. Seasonal variation in diel activity and microhabitat use of an
550   endemic New Zealand stream-dwelling galaxiid fish. Freshwater Biology. 2003;48:1765-
551   1781.
552   57.   Hickey MA, Closs GP. Evaluating the potential of night spotlighting as a method for
553   assessing species composition and brown trout abundance: a comparison with
554   electrofishing in small streams. Journal of Fish Biology. 2006;69(5):1513-1523.
555   58.   West DW, Jowett IG, Richardson J. Growth, diet, movement, and abundance of adult
556   banded kokopu (*Galaxias fasciatus*) in five Coromandel, New Zealand streams. New Zealand
557   Journal of Marine and Freshwater Research. 2005;39(4):915-929.

558 59.   Joy MK, Death RG. Control of freshwater fish and crayfish community structure in
559 Taranaki, New Zealand: dams, diadromy or habitat structure? Freshwater Biology.
560 2001;46(3):417-429.
561 60.   Swain NR, Reynolds JD. Effects of salmon-derived nutrients and habitat
562 characteristics on population densities of stream-resident sculpins. PLoS One.
563 2015;10(6):e0116090.
564 61.   Gałecki A, Burzykowski T. Fitting linear mixed-effects models: the lme()function. New
565 York, NY: Springer New York; 2012. 275-301.
566 62.   R Development Core Team. R: a language and environment for statistical computing.
567 R Foundation for Statistical Computing, Vienna, Austria; 2021. Available from:
568 https://www.R-project.org/.
569 63.   Fabozzi FJ, Focardi SM, Rachev ST, Arshanapalli BG. The basics of financial
570 econometrics: tools, concepts, and asset management applications: John Wiley & Sons, Inc;
571 2014.
572 64.   Symonds MRE, Moussalli A. A brief guide to model selection, multimodel inference
573 and model averaging in behavioural ecology using Akaike's information criterion. Behavioral
574 Ecology and Sociobiology. 2011;65(1):13-21.
575 65.   Nakagawa S, Schielzeth H, O'Hara RB. A general and simple method for obtaining R^2
576 from generalized linear mixed-effects models. Methods in Ecology and Evolution.
577 2013;4(2):133-142.
578 66.   Elith J, Leathwick JR, Hastie T. A working guide to boosted regression trees. Journal
579 of Animal Ecology. 2008;77(4):802-813.
580 67.   Fox J. Effect displays in R for generalised linear models. Journal of Statistical
581 Software. 2003;8(15):1-9.
582 68.   Cooke SJ, Martins EG, Struthers DP, Gutowsky LF, Power M, Doka SE, et al. A moving
583 target—incorporating knowledge of the spatial ecology of fish into the assessment and
584 management of freshwater fish populations. Environmental Monitoring and Assessment.
585 2016;188(4):239.
586 69.   Warren DR, Mineau MM, Ward EJ, Kraft CE. Relating fish biomass to habitat and
587 chemistry in headwater streams of the northeastern United States. Environmental Biology
588 of Fishes. 2010;88(1):51-62.
589 70.   Heggenes J, Northcote TG, Peter A. Spatial stability of cutthroat trout (*Oncorhynchus
590 clarki*) in a small, coastal stream. Canadian Journal of Fisheries and Aquatic Sciences.
591 1991;48(5):757-762.
592 71.   Spina AP. Habitat partitioning in a patchy environment: considering the role of
593 intraspecific competition. Environmental Biology of Fishes. 2000;57:393-400.
594 72.   McIntosh AR, Townsend CR. Interpopulation variation in mayfly antipredator tactics:
595 differential effects of contrasting predatory fish. Ecology. 1994;75(7):2078-2090.
596 73.   Baker CF. Lateral line and olfactory sensory systems in the biology of the banded
597 kokopu *Galaxias Fasciatus*. PhD thesis, University of Auckland, Auckland, New Zealand;
598 2000.
599 74.   David BO, Stoffels RJ. Spatial organisation and behavioural interaction of giant
600 kokopu (*Galaxias argenteus*) in two stream pools differing in fish density. New Zealand
601 Journal of Marine and Freshwater Research. 2003;37(2):315-322.
602 75.   Bonnett ML, Lambert PW. Diet of giant kokopu, *Galaxias argenteus*. New Zealand
603 Journal of Marine and Freshwater Research. 2002;36(2):361-369.

604   76.   Rosenfeld J, Porter M, Parkinson E. Habitat factors affecting the abundance and
605   distribution of juvenile cutthroat trout (*Oncorhynchus clarki*) and coho salmon
606   (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences. 2000;57(4):766-
607   774.
608   77.   Armstrong JD, Kemp PS, Kennedy GJA, Ladle M, Milner NJ. Habitat requirements of
609   Atlantic salmon and brown trout in rivers and streams. Fisheries Research. 2003;62(2):143-
610   170.
611   78.   Roni P, Beechie T, Pess G, Hanson K, Jonsson B. Wood placement in river restoration:
612   fact, fiction, and future direction. Canadian Journal of Fisheries and Aquatic Sciences.
613   2015;72(3):466-478.
614   79.   Henderson MJ, Iglesias IS, Michel CJ, Ammann AJ, Huff DD. Estimating spatial-
615   temporal differences in Chinook salmon outmigration survival with habitat- and predation-
616   related covariates. Canadian Journal of Fisheries and Aquatic Sciences. 2019;76(9):1549-
617   1561.
618   80.   Kawaguchi YN, S. Contribution of terrestrial invertebrates to the annual resource
619   budget for salmonids in forest and grassland reaches of a headwater stream. Freshwater
620   Biology. 2001;46:303-316.
621   81.   Baxter CV, Fausch KD, Carl Saunders W. Tangled webs: reciprocal flows of
622   invertebrate prey link streams and riparian zones. Freshwater Biology. 2005;50(2):201-220.
623   82.   McDowall RM. The composition of the New Zealand whitebait catch, 1964. New
624   Zealand Journal of Science. 1965;8(3):285-300.
625   83.   Schmitt RJ, Holbrook SJ. Gape-limitation, foraging tactics and prey size selectivity of
626   two microcarnivorous species of fish. Oecologia. 1984;63(1):6-12.
627   84.   Quinn JM, Cooper AB, Davies-Colley RJ, Rutherford JC, Williamson RB. Land use
628   effects on habitat, water quality, periphyton, and benthic invertebrates in Waikato, New
629   Zealand, hill-country streams. New Zealand Journal of Marine and Freshwater Research.
630   1997;31(5):579-597.
631   85.   Penaluna BE, Dunham JB, Noakes DLG. Instream cover and shade mediate avian
632   predation on trout in semi-natural streams. Ecology of Freshwater Fish. 2015;25(3):405-411.
633   86.   Parsons DM, Middleton C, Smith MD, Cole RG. The influence of habitat availability on
634   juvenile fish abundance in a northeastern New Zealand estuary. New Zealand Journal of
635   Marine and Freshwater Research. 2014;48(2):216-228.
636   87.   Halpern BS, Gaines SD, Warner RR. Habitat size, recruitment, and longevity as factors
637   limiting population size in stage structured species. The American Naturalist.
638   2005;165(1):82-94.
639   88.   Merz J, Caldwell L, Beakes M, Hammersmark C, Sellheim K. Balancing competing
640   life-stage requirements in salmon habitat rehabilitation: between a rock and a hard place.
641   Restoration Ecology. 2018;27(3):661-671.
642   89.   Leathwick J, Julian K, Elith J, Rowe D. Predicting the distributions of freshwater fish
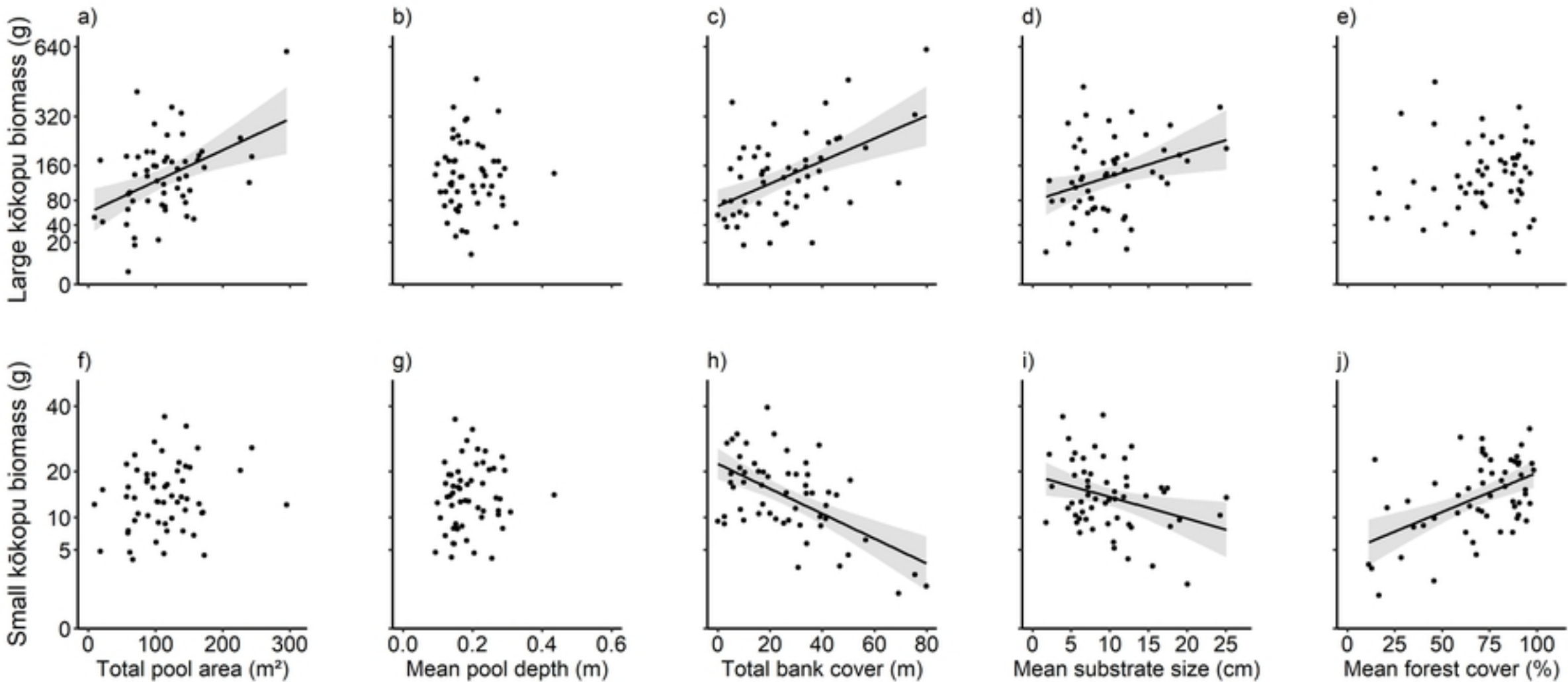643   species for all New Zealand's rivers and streams. 2008.

Fig1