Ministry for Primary Industries
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Feasibility of longfin eel stock assessment

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Growing and Protecting New Zealand

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EXECUTIVE SUMMARY

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This study explores how modelling may be used in future to determine the stock status of New Zealand longfin eels. I examine in particular the GIS-based method used by Graynoth and others (Graynoth et al. 2008; Graynoth & Booker 2009) (GJB), and stock assessment-based approaches (Dunn et al. 2009; Fu et al. 2012). In addition, I identify potential improvements in some of the analyses used in the GJB approach, and revise some of these analyses.

My review of the GJB approach found that such GIS-based approaches are reasonable, and that the GJB study provides a useful foundation for further work. The focus on habitat is appropriate because eels are strongly habitat-dependent and size patterns, densities, and sex ratios vary substantially at local scales. The estimates of original biomass were based on invalid assumptions about population length structure. The methods used to estimate current biomass can be made more reliable and potentially useful, by correcting problems, and with additional work to address important gaps. Sex ratio was not considered in sampling or models, which is problematic because eel sex ratios differ between fished and unfished areas, and maintaining female spawning biomass is a primary management objective. Productivity was also not considered, which is important because growth rates vary considerably among sites and are likely to differ between fished and unfished areas. They did not consider density variation between catchments, which my reanalysis indicates is substantial and important. Sampling data are only available for a few catchments, so extending the analysis across New Zealand will require alternative methods and probably additional sampling.

Stock assessment modelling methods are more problematic. Eel stocks are fractal, highly fragmented and unmixed at the population scale, with highly variable population parameters between locations. The fished part of the population will have, on average, different population parameters (sex ratio, density, growth rates) from the unfished part.

A model to estimate or index female eel spawning biomass will therefore need to start with a GIS-based approach. Management requires inferences about the unfished part of the population as well as the fished part, since the unfished part is the source of most female reproductive output. Even estimates of relative spawning biomass after exploitation, when considered at the population level, will require assumptions or estimates of the spatial distribution of the population across the available habitat, including the distributions of biomass, productivity, and sex ratios.

Long-term monitoring and modelling of spawning biomass will need to prioritise the unfished areas that generate more female spawning biomass. Monitoring requires fishery-independent data, as used in the GJB and Beentjes et al. (in press) approaches. Longfin eels are very long-lived so approaches that provide a point estimate are reasonable in the short term, but long term monitoring will need to consider temporal effects as well. Models and sample datasets that allow the prediction of sex ratio and productivity should also be developed. Existing datasets may be used to develop simple models that are better than the current default assumptions of uniform productivity and sex ratio.

Estimation of spawning biomass may use a variety of data inputs, including data from the New Zealand Freshwater Database (NZFWDB), site-specific catch data, and additional targeted sampling. Sampling is expensive, so should be carefully designed to maximise the precision of management indicators, and to minimize costs. Designing additional sampling may require an appropriate model to be developed first, so that analysts can assess which factors contribute to variability. The modelling approach used will require further development.

1. INTRODUCTION

The commercial freshwater eel fishery in New Zealand developed in the late 1960s. Landings consist of the endemic longfin eel (*Anguilla dieffenbachii*), and the shortfin eel (*A. australis*) which is also found in southeast Australia. Total New Zealand annual eel catches peaked in 1972 at 2077 t and averaged about 1300 t from 1972 to 1999, with fluctuations but no clear trend. From 1999, catches progressively declined to a low of about 520 t in 2008–09 and have since gradually increased to 715 in 2012–13. In recent years, the catch has been evenly split between the North and South Islands, with shortfin the dominant species in annual landings (87% and 60% in the North and South Island, respectively). The 2012–13 longfin catch was 230 t of which 164 t was landed from the South Island and 67 t from the North Island.

Longfin eels are considered more at risk of overfishing than shortfin because they are endemic to New Zealand and spawn at a considerably older age, for both sexes. The longfin females are considered to be more at risk of the effects of overfishing, and sustainability depends on there being sufficient numbers of females escaping to migrate and spawn each year. Longfin eels are found further inland than shortfin eels, occupying high country streams and lakes. For the longfin eels in some catchments, both upstream and downstream passage have been compromised by hydro-electric dams, significantly reducing the amount of available habitat above these hydro schemes for longfins to grow and reach spawning sizes. Graynoth et al. (2008a) estimated that as much as 6000 t of longfin eels is contained in hydro reservoirs. Trap and transfer schemes operate that mitigate the effects of these hydro dams, but it is unknown how effective these schemes are (i.e., what proportion of the total number of fish reaching the site are captured and survive during up-stream and down-stream migrations).

A comprehensive review of freshwater eel research in New Zealand was carried out in November 2013 (Haro et al. 2015). The Geographical Information Systems (GIS) based estimates of biomass by Graynoth et al. (2008) were reviewed and the expert panel recommended that further development is required before the adequacy and relevance of these results can be evaluated for the management of the stock. The panel were not presented with the conventional age and length structured population models carried out for Southland and New Zealand wide respectively (Dunn et al. 2009; Fu et al. 2012), and hence they made no comment on the efficacy of these models or recommendations for future work.

2. RELEVANT PAST RESEARCH

2.1 Conventional stock assessment models

In 2006 the Ministry for Primary Industries (MPI) contracted the National Institute of Water and Atmospheric Research (NIWA) to investigate the feasibility of a population model for longfin eels. The outcome was the development of a conventional, age structured population dynamics model for longfinned eels in Southland, the area for which the most comprehensive data was available (Dunn et al. 2009). Two spatial model structures were investigated— single-area and two-area. The single-area models ignored that part of the population believed to reside in closed areas or areas that otherwise had lifelong protection from fishing. The two-area models assumed a constant proportion of recruitment to a closed protected area. Current spawning stock biomass for Southland was estimated to be either about 5% or 20–25% of virgin biomass, depending on whether a single-area or a two-area model was used. Simple projection suggested that, for the single stock models and at current catches, the Spawning Stock Biomass (SSB) estimates from most models stayed at similar levels or declined slightly.

Subsequently, in 2009 a length structured population model with two spatial model structures was investigated for Southland and for New Zealand as a whole (Fu et al. 2012). Estimates from the New Zealand wide feasibility models suggested that the pre-exploitation female spawning stock biomass was

about 1700 t, with a biomass of legal sized eels of about 16 000 t in all fished areas, and about 6000 t in the protected area. Current female spawning stock biomass was estimated to be about 55% of the pre-exploitation level. The New Zealand model estimates of current legal sized eels in the fished areas ranged from 20% to 90% of the pre-exploitation level. Fu et al. (2012) found that changing from an age-based to a sized-based model improved the model fits, and better reflected the underlying biological processes of the longfin eel population. The model provides useful summaries of the exploitation histories in different areas and the current state of longfin eel populations, but only if the biological assumptions within the model are broadly correct and the simplifying assumptions are valid. Neither the length nor the age structured model was accepted by MPI as a tool for determining the current status of longfin eels, because it was considered that the models included too many assumptions on input variables such as growth, recruitment to each ESA, ageing reliability, density dependence, the proportions of eels that reside in protected areas, and the absence of anthropogenic activities.

More recently Alistair Dunn (NIWA) has carried out work for MPI on estimating longfin eel reference points Bmsy and Fmsy, i.e., the biomass and fishing mortality rate associated with the maximum sustainable yield. These reference points were investigated using a range of assumptions and an age based model. Model input parameters include growth, natural mortality, recruitment variability, steepness of the stock-recruitment relationship, weight at size, size at age, selectivity, and maturation. While this exercise does not provide estimates of current and unexploited biomass, it is useful for investigating "what-if" scenarios. The base model indicated that maximum sustainable yield will occur at a female SSB/Bo of around 30% at an exploitation rate of 5% (see PowerPoint presentation from EEL WG meeting EEL2013-12). This modelling approach has allowed investigation of how various input and productivity parameters affect Bmsy and the subsequent risk of falling below soft and hard limits. This work is ongoing and is currently being documented by Alistair Dunn.

2.2 Abundance as a function of environmental predictors

Graynoth et al. (2008) attempted to indirectly quantify or 'index' the longfin habitat in New Zealand based on field studies of the actual longfin biomass recorded from 212 sites from rivers and streams in Southland, Westland, Canterbury, Wellington, and Wanganui districts. To account for fishing pressure, abundance was adjusted by a simulated relationship between fishing pressure and the mean size of eels, further described below. They found that abundance was related to river flow and gradient. From this empirical relationship they estimated eel biomass throughout New Zealand using the information on flow and gradient for 500 000 numbered and linked reaches or segments contained in the River Environment Classification (REC). The resulting modelled biomass estimates were used as an indicator or proxy of the amount and distribution of habitat present for large female longfins.

Further, Graynoth classified waterways in New Zealand into five classes:
1) Waters closed to fishing that have egress for spawning females, e.g., national parks
2) Water protected in their upper reaches but where migrants can be fished further downstream
3) Water above dams or waterfalls where passage upstream and egress downstream are prevented.
4) Waters open to commercial fishing
5) Waters open to commercial fishing but not fished due to access or small size of waterway.
For each of these classes of water ways, Graynoth et al. (2008) estimated the biomass contained within.

The extent to which waterways were classified as Class 5 was estimated by modelling and extrapolating the location of effort around Wyndham (Southland). Small streams with flows of less than 0.5 $m^3.s^{-1}$ (cumecs) were rarely fished in this area. From 63 slope and flow records, Graynoth et al. (2008) modelled the likelihood that particular reaches would be fished and used this model to extrapolate across New Zealand with the assumption that this relationship applied nationally.

However, based on knowledge of the longfin catch from catchment-based Eel Statistical Area subareas collected as part of the project 'monitoring commercial eel fisheries' (Beentjes 2013), the extent of the areas categorised as fished in this study may have been over-estimated.

2.3 Estimation of longfin habitat and the proportion fished

MPI project EEL201401 (Beentjes et al. in press) has mapped, using GIS methods, commercial longfin eel fishing effort throughout New Zealand, and provided a representation of where and how often fishers set their nets. Interviews with 53 commercial eel fishers were used to identify fishing locations throughout New Zealand during the five-year period 2009–10 to 2013–14. All recorded fishing location information was georeferenced to individual segments of the River Environment Classification (REC2).

The total current longfin habitat in rivers was derived from 'probability of capture' models within REC2 segments, based on data from the New Zealand Freshwater Fish Database (NZFWFDB, McDowall & Richardson 1983). These data were previously analysed for the Independent Review of Eel Management (Haro et al. 2015) using generalised linear models, using both temporal and spatial variables to provide indices of temporal capture probability. They have subsequently been linked to detailed habitat information in the REC2 database, and analysed using random forest methods (Crow et al. 2014), but without a temporal component. This GIS-based approach was initially developed using boosted regression trees (Leathwick et al. 2008). Crow et al. (2014) developed separate estimates for three fishing methods (electrofishing, netting, and visual methods).

Habitat estimates in Beentjes et al. (in press) were expressed as wetted area (river segment length × mean width of segment at annual low flow (MALF)). Habitat in lakes was estimated using the proportions of lake areas that eels were thought to inhabit, which was usually the littoral zone. Fished habitat was expressed as the wetted area of fished river REC2 segments (or part thereof) and fished natural lakes to which longfins have unimpeded access. Habitat of lakes behind dams was excluded from current habitat available to longfins because of impeded access. Estimates of proportions of longfin habitat currently fished, virgin habitat fished, and loss of spawning biomass in New Zealand are based on these parameters.

3. SCOPE OF THIS PROJECT

The aim of this project was to evaluate the inputs and assumptions required for conventional stock dynamics or assessment models and to compare these with those required for the Graynoth GIS approach. The main aim was not to rerun these models, but to evaluate the assumptions associated with the input variables and conclusions that can be drawn from each model. The question we are asking is what additional information we need to know to have confidence that either model will give us something useful that can be used to understand stock status (i.e., current SSB relative to the virgin SSB) or other management or performance indicators.

For the population model, issues such as density dependence, depensation, density in closed areas, extent of protected areas, variable growth, variable recruitment, variable mortality (including natural, fishing, and other anthropogenic mortality), etc., have been proposed as important considerations for understanding eel stock dynamics. This paper assesses the extent to which these issues are supported by data from New Zealand or other studies in the international literature; where additional data collection may be required; and if and how such processes may be represented within a stock dynamics model. In addition, I will investigate how we may use simulation models as a means of further understanding their potential impact on a stock dynamics model. I will then draw this information together to provide a qualitative assessment as to the extent that standard population models may be sensitive to these issues.

The Graynoth model, while novel and innovative has not been well understood. This is because it employs methods that are not conventionally used in fisheries and some of the assumptions made are implicit – particularly the simulations and derivations used to provide biomass estimates for various categories of waterways. I look at the Graynoth model, and provide an explanation of the methods, assumptions made, and the efficacy of the approach. Although not initially expected to replicate and

rerun the Graynoth model, I was provided with the dataset by Eric Graynoth and was able to do so. I compare the approach with other, similar, approaches that are being developed in fisheries research departments/groups from Europe and elsewhere. In addition, I investigated those areas of the Graynoth model where assumptions may benefit from further validation.

Finally, I use the review of both approaches to develop recommendations about the feasibility of either approach or some combined approach as a means of developing estimates of stock status (i.e., current SSB relative to the virgin SSB) or other management or performance indicators.

4. DATA SOURCES

Data collection methods were summarised by the independent review of eel management (Haro et al. 2015). The relevant section is adapted below:

4.1 Standardised Catch per Unit Effort (CPUE)

Indices of abundance, based on standardised CPUE, are produced for the commercially targeted portions of eel populations within each eel quota management area (ANG QMA). The CPUE indices are updated on a 3-year cycle. Although the ANG QMAs of the South Island are composed of both shortfin and longfin eels, separate indices of abundance are produced for each species. CPUE analysis is done at the spatial resolution of Eel Statistical Areas (ESAs). Each QMA consists of multiple ESAs and in most cases the ESA providing most of the catch is used to produce an index of abundance for the QMA. In some instances (e.g., ANG 15) two indices of abundance are calculated, as both ESAs support important fisheries. Low numbers of active permit holders, inconsistent participation across years after the introduction of eels into the QMS, and generally low overall catch and effort activity resulted in unreliable/poor indices of abundance after 2001 for several South Island QMAs.

4.2 Elver Recruitment

Annual counts of the elvers of each species passing hydro-electric power dams on several rivers are recorded by stakeholders. Eels recruit into rivers as transparent glass eels in their first year of life and spend some time in estuarine reaches before moving upstream. Elvers (about 150 mm long), the next stage in the life-cycle, are 1–6 years old and move upstream as they grow older. Elvers entering the traps at sampling sites therefore comprise more than one year-class, with the number of year classes in the sample and average size/age increasing with the distance of the dam/site from the mouth of the river. Elver catch indices at dams are thought to provide a long term indication of recruitment trends.

4.3 Size Composition

Proportions of the catch of each species falling into market-related size categories are provided by all major Licensed Fish Receivers (LFRs) that process eels. The data are provided annually at a sub-ESA spatial resolution related to catchment. Increasing rates of exploitation are expected to result in higher proportions of the catches of each species in smaller size categories. There is sometimes less market demand for eels in the medium size category, with the result that eels in this category are often avoided or released.

4.4 New Zealand Freshwater Fish Database (NZFWFDB)

This is a voluntary database containing a substantial quantity of research data (about 35 000 observations), beginning in 1960. It is mostly presence/absence data collected using electric fishing by a variety of organisations including NIWA, the Department of Conservation (DOC) and Regional Councils.

4.5 Electric Fishing Size Composition Data

Regional Councils and NIWA have a substantial quantity of length frequency data for both longfin and shortfin eels collected by electric fishing in wadeable streams.

5. EEL POPULATION DYNAMICS

Every modelling approach involves assumptions that may strongly affect the resulting stock status estimates (i.e., current SSB relative to the virgin SSB). For managing eel populations, issues such as stock mixing, density dependence, depensation, density in closed areas, extent of protected areas, variable growth, variable recruitment, variable mortality (including natural, fishing, and other anthropogenic mortality), etc., are important considerations. Although there are differences in details and parameter values (such as mean growth rates and size at maturity) between species, eels are believed to share similar life history patterns across most of these factors. In the following section I discuss how these characteristics may affect different types of modelling approach, and examine evidence from all species of *Anguilla*, including evidence for New Zealand longfin eels where possible.

5.1 Stock mixing and movement

Stock mixing is a particularly important issue for stock assessment-based approaches, while the other approaches being considered here do not assume population mixing. In their most common form, stock assessment models assume that the entire population is part of one fully-mixed stock. This is a simplifying assumption that allows observational data such as CPUE or size information to be informative about the entire stock and, similarly, implies that removals via catch apply the same level of fishing mortality across the entire stock. Of course, mixing is rarely complete in any modelled population, but assuming such a unit stock may be reasonable if fishing effort is relatively evenly distributed across the stock, if population parameters such as growth and mortality are relatively uniform, and if the samples used in the model are representative of the stock as a whole. It is also possible to model a stock as a number of interconnected subpopulations with movement between areas. In this case the equivalent assumptions of full instantaneous mixing apply at the subpopulation scale.

Where mixing is not complete and any of the important population parameters differ, it is generally necessary to model the differences between areas explicitly. Averaging across parameters such as growth rates or exploitation rates will provide unreliable estimates. For example, consider a population with two equal areas in which one area is exploited at 20% per year, and the other is not exploited at all (ignoring natural mortality). After 10 years the combined population would be at 55% of virgin stock size. However, applying the average mortality of 10% per year to a single stock would suggest a reduction to 35% of virgin.

Movements may to some extent be density-dependent, and also dependent on local conditions such as barriers, substrate, and flow. Density-dependent movement is potentially important for all types of population modelling, even those without spatial structure, because it changes how fishing mortality affects the population. Density-dependent movement affects the rates of mixing between fished and unfished areas, and the rates of recovery of recently fished areas.

A key point about freshwater eel populations, including the New Zealand longfin eel population, is that the available evidence suggests that they are at the very unmixed end of the population spectrum. Their distribution is fractal, extending from sea up river catchments into countless small streams and ditches, and mixing appears to be low except at local scales (i.e., within lakes). After glass eels recruit to individual catchments, there may be effectively no subsequent mixing between the eels in different catchments until the mature eels emigrate to spawn many years later. At smaller scales such as within catchments, mixing is also likely to be limited. The local scale at which mixing does occur is difficult to determine and no doubt depends on multiple factors such as habitat, age and size structure, population

density, connectivity, and environmental conditions. Temporal scales of movement are also not well determined, but appear to be long. Longfin eel generation times are measured in decades.

Eel movement is not well understood, but four distinct behaviour types have been suggested: 'founders' that colonize rivers until they settle in the first available suitable habitat they encounter; 'pioneers' that migrate upstream to the upper boundaries of the system; 'home range dwellers' that establish in a given area for several months to several years; and 'nomads' which are erratic eels that perform a general upstream shift as they search for suitable areas to forage or to settle (Ibbotson et al. 2002). However, the average movement is the most important concern for modelling, and on average eel movements follow a diffusive pattern (Ibbotson et al. 2002). Since eels first enter freshwater at the bottoms of catchments, mean age and size tend to increase with distance from the sea, while population densities decrease (Ibbotson et al. 2002; Yokouchi et al. 2008).

Some relatively long movements must occur to repopulate places previously fished by commercial fishers (Jellyman & Sykes 2003). A small proportion of 9956 streamer-tagged *A. australis* in Lake Ellesmere / Te Waihora moved far enough that they could at least partly repopulate harvested areas within the same growing season, but the majority were captured at or close to their release site. Eels may move more widely within lakes than in rivers.

However, there is considerable evidence that average movement rates are low, and that individuals are often site-attached. Relocated eels have often been found to return to their original location even over long distances (Tesch 1967; Parker 1995; Jellyman et al. 1996; Lamothe et al. 2000). In small New Zealand streams radio-tracked eels moved an average distance of less than 2 metres per day, with eels often found in one location for extended periods (Jellyman & Sykes 2003), although these eels may have ranged more widely between observations and returned to a favoured resting location. Chisnall & Kalish (1993) released 47 New Zealand eels of both species, and over 3 years recaptured 16 of them within 20 m of their original capture site. Such movement estimates depend on the distribution and intensity of recapture effort, which were not described, but still suggests that a high proportion of eels do not mix into other areas. Experimentally depleted reaches of a stream in Spain took up to 2 years to recolonise (Lobon-Cervia et al. 1990). In New Zealand, a stream in relatively unexploited condition was subsequently exploited for 4 years, and allowed to recover for 5 years (Chisnall et al. 2003). It recovered its eel biomass after 5 years, but the shortfin proportion of eel biomass increased from 25% to 50%. In three New Zealand streams over 3 years, size distributions of both eel species varied little between years, indicating little movement between reaches (Glova et al. 2001).

5.2 Density dependent productivity

Density dependence is important in population models because it affects population structure and the size of the population at equilibrium, and resilience to exploitation. Many marine fishery models include density-dependence only in the stock recruitment relationship (e.g., the Beverton-Holt SRR), which is sufficient in many cases. In some populations however, density-dependence operates strongly through other parameters such as growth, age/size at reproduction, or natural mortality. When these processes affect the adult stages of the population, after recruitment, they can bias the population model. Density dependent processes may be important in eel population modelling because the fishery is likely to favour areas with higher yields and densities, and samples in these areas may be unrepresentative of growth and mortality rates in lower density areas.

The scale at which density-dependence operates is important, because modelling density-dependence requires information or assumptions about carrying capacity. Density-dependence effects on growth, mortality, and sex-determination operate at a local scale in eels, which is problematic for stock assessment modelling, since it is not practical to estimate the carrying capacities of multiple sub-stocks.

Density dependence may affect many aspects of eel population dynamics, though its effects are not well understood. Eel growth can be density-dependent (Horn 1996), and this has been demonstrated in some experimental studies (e.g., Roncarati et al. 1997), but Aprahamian (2000) found no relationship between growth rate and density or biomass in the Severn river. Food availability can also affect density, which makes the relationships difficult to interpret. Density dependent mortality is difficult to detect, but has been observed in European (Vollestad & Jonsson 1988; Bevacqua et al. 2011) and New Zealand eels (Graynoth et al 2008).

5.3 Sex ratio and length at maturity

Eel sex ratio varies spatially, and this has implications for eel stock assessment and management. A major objective of fishery management is to maintain female spawning biomass, and so the interactions of fishing mortality and sex ratio are very important. In addition, the life histories of males and females are very different, with males migrating at a much smaller size and younger age than females. This issue affects stock assessment approaches, because local fishing mortality has far more impact on local female spawning biomass than on males (Dekker 2000b; Hoyle & Jellyman 2002), and because fishing pressure is likely to be unevenly distributed with respect to sex ratio (see below). Models fitted to size data must also take into account the local sex ratio because it will affect the expected size distribution.

Spatially varying sex ratio also affects GIS-based approaches, because the sex ratios are expected to be more female-biased where densities are lower (Davey & Jellyman 2005; see review in Robinet et al. 2007). If fishing effort is higher in areas with higher eel densities, then estimates of the fished proportion of habitat may overestimate the impact of fishing on female spawning biomass.

The sex of eels is mainly determined by environmental factors, and at high densities most eels differentiate into males (Davey & Jellyman 2005; Geffroy & Bardonnet 2015). Sex may also be strongly determined by growth rates at small sizes, with faster early growth associated with male sex (Roncarati et al. 1997; Davey & Jellyman 2005). There are broad-scale spatial patterns in eel sex ratio, with eels in the upper reaches of rivers predominantly female, and males more abundant in the estuaries and lower parts of rivers (Helfman et al. 1987; Ibbotson et al. 2002). Sex ratios can also vary through time (Jellyman & Todd 1998; Davey & Jellyman 2005). For example, during the early 2000s the longfin populations of a number of southern South Island rivers became dominated by males, possibly because depletion of large females by fishing pressure led to higher densities of small eels, which favoured differentiation to male sex (McCleave & Jellyman 2004).

5.4 Depensation

Depensation occurs when the per-capita population growth rate decreases as the density or abundance decreases to low levels (Liermann & Hilborn 2001). The spawning biomass targets employed in most fishery management (i.e., 20% or 30% of unfished) should be sufficient to maintain the stock above the level at which depensation occurs. Stock assessment models usually include a stock recruitment relationship that does not allow for depensation, so this is potentially an issue for stock assessment approaches.

Depensation may occur via four main mechanisms: reduced probability of fertilisation, impaired group dynamics, conditioning of the environment, and predator saturation. For eels, fertilisation occurs after migration from the whole population to the spawning ground, so this effect is likely to occur at the scale of the population. Depensation has been proposed as a mechanism for the observed declines in recruitment of European eels (Dekker 2003). However, low recruitment also causes low stock size, the factors affecting eel recruitment are poorly understood, and spawning in the wild has rarely been observed, so it is difficult to provide evidence either for or against depensation.

5.5 Density in and extent of protected areas

Identifying areas with no fishing mortality, and quantifying the biomass, sex ratio, and productivity in those areas, is important for all assessment methods, including those based on stock assessment and on GIS approaches. Protected areas are a particularly important type of unfished area because there is more certainty of long-term freedom from fishing mortality.

The spatial distribution of commercial fishing effort in New Zealand has recently been quantified (Beentjes et al. in press), and the proportion of currently unfished habitat has been estimated. The distributions of customary and recreational fishing effort have not been quantified, and nor has the historical distribution of commercial fishing effort. Eels, and particularly female eels, spend decades in freshwater before reaching maturity, so the effects of historical fishing effort are still important for spawning output.

5.6 Recruitment variability

Recruitment variability is generally large in marine fish populations. In traditional marine fishery stock assessment methods, recruitment is usually directly estimated because it is such an important source of variation, and drives population trends. High recruitment variability affects stock assessment, particularly if there are time-area interactions, which make it much more difficult or even impossible to estimate year effects. It also affects any method using population size structure to infer fishing mortality based on equilibrium assumptions, because it increases natural size variation.

Recruitment variability in eel populations both in New Zealand and internationally is high, within and between years, and between regions (Francis & Jellyman 1999; Jellyman et al. 2002; Acou et al. 2009). Temporal variability introduces size variation into the population (Francis & Jellyman 1999), which makes it more difficult to use size data to make inferences about total mortality. Analyses in New Zealand with both eel species (Jellyman et al. 2002) did not find significant year-area interactions in glass eel abundance, though sample sizes may have been too small to detect differences. Glass eel abundances in two US estuaries were asynchronous or weakly synchronous over 16 years (Sullivan et al. 2006).

5.7 Growth variability

Somatic growth rates are important in stock assessments, since they affect productivity, the ages at recruitment to the fishery and at maturity, and the fit of size data in the population model. When growth rates differ between parts of a stock, it can be misleading to model the areas together.

Growth rates of New Zealand eels are characterised by high variability, both within and between populations and habitats (Horn 1996; Jellyman 1997). Similarly, high growth variability within and between habitats has been found for other eel species (Walsh et al. 2006; Yokouchi et al. 2008). Growth rates tend to be higher in more productive habitats, such as estuarine areas (Morrison & Secor 2003; Walsh et al. 2006), and lakes (Yokouchi et al. 2008). In the Waikato River, longfin growth rates are faster in pastoral streams than in forested streams (Chisnall & Hicks 1993). Long-term (but not early) growth rates of females are generally faster on average than those of males (Jellyman 1997; Oliveira & McCleave 2002; Davey & Jellyman 2005). Growth rates and feeding habits of eels have also been shown to change with size in Lake Ellesmere as the fish shift from an invertebrate dominated diet to a piscivorous one (Kelly & Jellyman 2007).

5.8 Spatial size variation

Spatial size variation affects population models that make inferences from size structure in an area. Stock assessment models are often fitted to size structure data, and assume the same structure throughout the population or sub-population. Ignoring existing spatial structure will lead to biases, though this can be reduced in some circumstances by defining multiple fisheries (Hurtado-Ferro et al. 2013). For example, Graynoth et al. (2008) combined their GIS-based models with sampled size distributions and used current mean length and assumptions about selectivity to infer original biomass, assuming the same equilibrium length at all sites. Spatial size variation will cause these estimates to be biased.

There is considerable evidence that eel size structure varies between habitats, with population density, and with distance from the sea. In three New Zealand streams, longfin size distributions differed significantly between streams and to a lesser extent between reaches (Glova et al. 2001), while shortfin sizes varied substantially between both streams and reaches. Neither species showed statistically or biologically significant change in size distribution between years. Numbers of small eels declined with distance upstream. There is also evidence of size-based differences in habitat use (Glova & Jellyman 2000). Japanese eels show significant differences in population structure between habitats (Yokouchi et al. 2008). European eels also show significant differences in habitat preference according to eel size (Laffaille et al. 2003; Laffaille et al. 2004; Lasne & Laffaille 2008).

Such spatial size variation may have various causes. The rates of diffusion upstream mean that there are fewer small eels further from the sea. Habitat structure such as water depth, flow rate, and size of available cover such as cobbles can all affect the sizes of eels occupying the habitat, and also the catchabilities at size (i.e., fishing selectivity) of the eels present. Sex ratios can also affect size distribution because females mature and emigrate at much larger sizes than males. The presence of large females may suppress the numbers of smaller eels, through cannibalism or avoidance. Time-varying recruitment that is not spatially uniform will also cause spatial size variation.

5.9 Mortality variability

Spatial variation in fishing mortality has similar implications for population modelling to most of the other spatially varying aspects of eel population dynamics already discussed. It also interacts with factors such as spatially varying growth rates and low mixing rates.

To obtain information on spatial variation in fishing pressure at a scale, Beentjes et al. (in press) have mapped fishing effort across New Zealand. Fishing occurs mainly in rivers, with smaller contributions in natural and hydro lakes. Fishing intensity per REC2 segments range from 0.2 to 5.5 fishing events per year. In some segments this is conservative, because multiple passes per year by individual fishers were not taken into account (Beentjes et al. in press). There are also areas that are not currently fished though they may have been fished in the past, and other areas that have rarely or never been fished. Reasons for the high variability in fishing effort are not described, but may include ease of access, relative catch rates, commercial demand for the available sizes, and higher recovery rates for some areas that may have more movement than others.

This high variability in fishing effort is likely to cause high variability in fishing mortality between areas.

6. REVIEW AND ANALYSIS OF POTENTIAL APPROACHES

6.1 Graynoth GIS-based methods

Using GIS-based methods to estimate biomass is a logical approach for a species that is highly dependent on habitat availability. These methods rely on identifying relationships between habitat variables and the variables of interest (e.g., longfin eel presence, longfin female biomass), and obtaining a broadly-based habitat dataset that reports these habitat variables.

In New Zealand, probably the first approach along these lines was by Broad et al. (2001), who developed a logistic regression model to predict the occurrence of longfin eels. Similar approaches have been used internationally (e.g., Van De Wolfshaar et al. 2014).

Since all eels begin life in the sea, access is important for modelling eel distribution. Thus purely habitat-based models are unlikely to be ideal. Smogor et al. (1995) suggest that parsimonious, large-scale models (e.g., diffusion models) may predict the distribution and abundance of American eels more reliably than do more typical, small-scale habitat models (e.g., habitat suitability models). Modelling spatial patterns based on observations will be important, because accessibility varies between and within catchments. Some are completely blocked by natural and anthropogenic structures, other barriers will reduce but not eliminate access, and some habitat types may act as cryptic (to us) barriers to upstream movement for eels. Environmental variation such as droughts or floods may permit access intermittently to areas that are normally inaccessible to upstream movement.

6.1.1 Methods

I investigated the methodology used in the Graynoth et al. (2008) (GJB) and Graynoth &Booker (2009) GIS approaches for the evaluation of stock status for longfin eels, in order to identify implicit assumptions that are currently not well understood. I met with Eric Graynoth to develop an understanding of how the models work, and to identify the possibility of re-running some of them. He provided a copy of the stream and river eel density database together with advice on its structure, and we discussed options for further exploring the dataset. I subsequently explored uncertainty in the model outputs by examining model sensitivity to alternative parameterisations.

The dataset

The stream and river dataset is described by GJB, but I repeat important points here in order to identify potential issues. The data were collected during field surveys using electrofishing (Graynoth & Niven 2004; Graynoth et al. 2008). Sites were selected using stratified random sampling, though with some bias in the selection, given that "sites tended to be grouped within particular catchments and were usually located near a road bridge or were accessed over farmland using four-wheel drive vehicles. Only sites that could be electric fished were selected for study." (Graynoth et al. 2008). The database includes 212 sites.

Estimation of original biomass

GJB used the mean lengths of harvestable eels as an index of the effects of commercial fishing on eel biomass. They related the proportion of original biomass present (Y) to the mean eel length in metres (L) using the equation $Y = 30.74L^{6.074}$. This relationship between mean size and depletion level was determined by populating a simulation model of eel population dynamics (Hoyle & Jellyman 2002; McCleave & Jellyman 2004) with data from the Aparima River (Jellyman et al. 2000; McCleave & Jellyman 2004). The model assumes equilibrium with constant harvest rate and recruitment. It also assumes that growth rate, natural mortality, and sex ratio at length (each of which affect mean size) within each sampled site are the same as the Aparima River. As acknowledged by GJB, mean size is likely to vary among sites within, and outside the Aparima, due to factors other than fishing pressure. I examined the potential for this variation to affect the estimates of original biomass.

The standardization model

The stream and river data were analysed by GJB using generalized linear and generalized additive models in S-Plus (Insightful 2001). The data were analysed with a log link and using quasi-likelihood with variance=mu, so that variance was modelled as proportional to the mean. For model selection they used the percent deviance explained and Akaike Information Criterion (AIC) (Akaike 1973; Burnham & Anderson 2002). Their method for calculating AIC [AIC = log (Residual Deviance/n) + 2K, where n = number of samples and K is the degrees of freedom] probably gave reasonable results but was not strictly correct, because it assumed that residual deviance was based on likelihood and that variance was constant (section A2.4, GJB). In fact, quasi-likelihood is not equivalent to log-likelihood and such models rarely provide AIC. The GJB modelling approach also assumed that variance was proportional to the mean, which may not have been correct.

GJB modified their selected models based on knowledge of the biology of eels, and interpreted their results based on the plausibility of trends in the modelled terms. The final models chosen for both current and original biomass were simpler than the best models based on AIC. The final models included smoothing splines fitted to just two parameters: mean annual low flow (MALF), and stream gradient.

Given the importance of these models for inferences about total biomass, I reanalysed the data using updated methods. I applied generalized additive models using the package mgcv (Wood 2011) in R (R Core Team 2014). I log transformed the mean low flow and slope terms before fitting, given the apparent relationship (see figures A1.6 and A1.7 in GJB). In addition to the two variables selected by GJB I explored models that included the covariates altitude, temperature, shade, and distance to sea, and categorical variables region, geology, land cover, and river.

For model selection I used the Generalised Cross-Validation (GCV) statistic, with better models having lower GCV values. I also fitted the models using the likelihood-based Tweedie distribution, which provides AIC and estimates the relationship between mean and variance, and indicated that variance was proportional to the mean to the power of 1.5.

6.1.2 Results

I updated the standardization model of eel current biomass as a function of covariates. Log transforming the slope and flow variables improved model fit, based on residual distributions and model selection criteria (Table 1, Figure 1, and Figure 2). Quasi-likelihood and Tweedie models gave similar model selection results, and the quasi-likelihood results are presented below.

Including region (and mean summer water temperature) as well as log slope and log flow improved the model, indicating that each region had its own characteristics that could not be inferred from slope and flow alone. However far more improvement was achieved by fitting a 'distance from sea' variable for each river – this was the most influential effect in the model (Figure 3). The distance to sea effects were large enough that they are likely to change the predicted outputs of national eel biomass. Predictive power was considerably better for the updated models (see lower right panels in Figure 1 and Figure 2). The best model identified was:

CURRLF ~ s(log(LOWFLOW)) + s(log(SLOPE)) + s(DISTSEA, by = RIVER.) + s(STEMP)

6.1.3 Discussion

GIS-based approaches, such as the approach used by GJB, are reasonable methods to try to estimate current eel biomass. The approach considers habitat availability, which is appropriate because eels are strongly habitat-dependent, and size patterns, densities, and sex ratios vary substantially at local scales. It also considers the important issue of access by including distance from the sea. The fishery-

independent sampling process collects data from unfished areas, which is vital because these are the areas where the majority of female spawning biomass is produced.

There are some problems with the method as originally applied by GJB, and some gaps that will need additional work to address. Sex ratio was not considered in the sampling or the models, which is problematic because sex ratios vary markedly between fished and unfished areas, and maintaining female spawning biomass is a primary management objective. Including sex ratio would require a model of the relationships between habitat variables and sex ratio, and some data with which to parameterise it. A simple model based on the proportion of females increasing with distance from the sea or altitude would be an improvement on the default assumption of 50:50 sex ratio.

The original models also did not consider variation between catchments, and the reanalysis here indicates that this variation is substantial and important. However, sampling data are only available for a few catchments, so extending this analysis across New Zealand is not currently possible without additional sampling.

The GJB approach aims to estimate both current biomass and original biomass, but the approach for estimating original biomass is problematic. It estimates original biomass by inferring fishing pressure from the current size structure, and extrapolating from current biomass. However, the size structure of eels in a given location is affected by local variables (see also the section above on population dynamics). It is unrealistic to try to estimate original biomass from current mean length without taking into account these local variables, which affect growth, mortality, and sex ratios. The implicit assumption of equilibrium at a particular place and time is also incorrect. The combined effects of these factors would substantially affect the estimates of original biomass. I therefore consider the approach for estimating current biomass to be more reliable and potentially useful.

The following points summarise factors that make it difficult to infer original biomass from current size structure:

A) The model's estimates of mean size assume that both recruitment and fishing pressure are uniform and constant even at a local level, and that sex ratios and growth rates do not vary spatially, so that the population reaches an equilibrium. However, eel fishing tends to be periodic, with each area fished and then left to recover. In addition, recruitment even at the catchment level varies substantially between years which may affect size distributions (Francis & Jellyman 1999). Size structure in a localised area (e.g., within stream reaches) will therefore depend on the time since it was last fished and the intensity of the fishing, the local growth rate, the rate of immigration of eels from surrounding areas, and the pattern of recruitment to the overall population.

B) Population size structure is affected by growth rates, which vary between areas and among eels within an area. Removing eels by fishing may increase the growth rates of those that remain or that colonise a fished-out area, due to density dependent effects. On the other hand, removing large eels may increase the recruitment and density of small eels by alleviating predation pressure, reduce mean growth rates across the remaining population, and make the sex ratio more male-biased.

C) Emigration of mature eels is important in size-structuring the population, but males emigrate much smaller and younger than females. Mean lengths may therefore be smaller in areas with a higher proportion of males, independent of the fishing pressure and biomass depletion.

D) Eel size structure tends to vary with distance from the sea, the substrate, water velocity, and availability of cover (Glova et al. 1998).

E) Sampled size structure may be affected by the substrate, fishing method, ways the fishing method is implemented, independent of the population size structure, since catchability at length is likely to depend on the availability of refuges.

The GJB method provides a single point estimate of current biomass, not considering changes through time, apart from changes between the original unfished state and the current state. Longfin eels are very long-lived so this approach is reasonable in the short term, but long term monitoring will need to consider temporal effects as well.

Index-based methods provide information on changes through time in population characteristics, such as density or size. Density trends are estimated by standardizing catch per unit effort (CPUE) data from commercial fishing and/or fishery-independent monitoring. Size trends are generally monitored from commercial catch data.

Currently, commercial CPUE trends are routinely monitored and standardized (Beentjes & Dunn 2013; Beentjes & Dunn 2015). This programme was reviewed by the independent review panel (Haro et al. 2015) who considered it comprehensive, well documented, and using appropriate methods. However, they identified some concerns, including changes in effort characteristics through time, changes in treatment of zero catches through time, lack of information on target species, potential hyperstability, and nonlinear relationships between catch and effort.

The main problem with CPUE as an indicator of population trends is that CPUE data come only from fished areas. In a poorly mixed population, indices from fished areas will be unrepresentative of the overall population trend. Furthermore, it is unclear what proportion of the population is indexed by commercial CPUE. During their freshwater growing phase, eel mobility appears to be relatively low, suggesting that fishing has mainly a local impact, but the spatial scales of eel movements are not well understood, and are likely to depend on local conditions and population structure. Movement may contribute to recovery of abundance and CPUE, through upstream movement and diffusion from surrounding areas, and there may be a density-dependent aspect to movement. Unfished areas that occur close to fished areas may contribute to recovery, but it is difficult to determine how much replacement biomass comes from unfished areas, and how much biomass remains in unfished areas.

Furthermore, the great majority of female spawning biomass is likely to be provided by unfished areas, and spawning contributions from fished areas are likely to be low, even given the effects of maximum size limits. CPUE indices for commercial areas are therefore not sufficient to address the most important concern – the long term maintenance of spawning biomass.

Estimating spawning biomass in both the fished and the unfished population requires analysis of fishery-independent sampling data, as in the GJB and Beentjes et al. (in press) approaches. Estimation may use a variety of data inputs, including data from the NZFWDB, site-specific catch data, scientific data, and additional targeted sampling. Data will continue to accumulate in the NZFWFDB, providing a foundation that can be added to with additional targeted sampling. Sampling is expensive, so should be carefully designed to maximise the precision of management indicators, and to minimize costs. Designing additional sampling should be preceded by development of an appropriate model, so that analysts can assess which factors contribute to variability, and which environmental conditions should be sampled.

The modelling approach used to estimate biomass of eels in New Zealand will require further development. The Beentjes et al. (in press) approach is promising but predicts probability of capture rather than probability of presence, and the three fishing methods used each have different probabilities of capture. Capture probabilities are strongly affected by sampling methodology and the reporting behaviour of different agencies (e.g., NIWA reports eels when observed, while Fish and Game focus on trout and are less likely to report eels) (Crow et al. 2014). Estimates will be strongly affected by changes in sampling methodology through time, and differences in method between personnel, agencies, and regions, which makes it difficult to reliably predict biomass. These issues will need to be addressed in future work. Models and sample datasets that allow the prediction of sex ratio and growth rate will also need to be developed.

6.2 Stock assessment-based methods

There has been debate and uncertainty about how and when stock assessment methods may be applied to eels. The Ministry of Fisheries Plenary Report (Ministry of Fisheries Science Group 2006) has reported that conventional stock assessment methods cannot be applied to eels (noting that "standard population models are inadequate to describe the unusual life cycle of freshwater eels"). This is broadly correct. However, this class of modelling approach is useful in some situations. There are a number of examples internationally, cited in the 2009 and 2012 reviews (Dunn et al. 2009; Fu et al. 2012). De Leo et al. (2009) reviewed eel modelling approaches and urged greater use of such strategies to compare management options. More recent examples include Tanaka (2014), who fitted an age and sex structured model to CPUE data using similar methods to European (De Leo & Gatto 1995) and American (Fenske et al. 2011) analyses.

The appropriate modelling approach depends on the objectives and the scope of the project. Here I consider appropriate uses for eel population dynamics modelling, and discuss whether the approach can be used to determine stock status (i.e., current SSB relative to the virgin SSB).

Assessment modelling approaches can be useful in settings with a relatively well-mixed water body (e.g., Dekker 1996; Dekker 2000b; Ciccotti et al. 2012), an approach that might be applicable to Lake Ellesmere/Te Waihora. In these situations, the effects of fishing pressure may be reasonably well distributed across the population, and sampling data has some chance of being representative of the population. Conventional approaches can then be used to estimate population parameters such as total biomass, spawning biomass, and fishing mortality within the water body.

Simulation approaches can also be used. In management strategy evaluation (MSE) an operating model is developed and used to test the potential impact of management interventions, or the utility of different research approaches. An operating model is a simulation model rather than an estimation model, and is not designed to determine the current status of a population.

Simple per-recruit approaches can be used in an MSE context to examine relative effects, without attempting to account for variability between areas and times, or to fit to observed data within the model. Such approaches have been used to make inferences about relative change in fished areas under different management systems, and the need for unfished areas (e.g., Hoyle & Jellyman 2002).

Population dynamics models that include estimation within the model may be useful for rough broad-scale estimates. For example, Dekker (2000c) applied an estimation approach across the European eel population, while acknowledging that results will be inaccurate and potentially misleading, because many of the underlying assumptions are not correct. Dekker (2000a) also noted the fractal nature of the European eel stock, and stated that this made 'the acquisition of exact and detailed knowledge of the total continental population simply impossible, and an up-to-date assessment of the European eel fisheries unachievable'.

The problems for stock assessment modelling of eels include the fractal, highly fragmented and unmixed nature of eel stocks, the high variability of population parameters between locations, and the fact that the fished part of the population will have, on average, different population parameters (sex ratio, density, growth rates) from the unfished part.

Developing a stock assessment model to estimate female spawning biomass, or relative spawning biomass, will therefore need to start with a GIS-based approach. A useful model of eels at the population scale needs to make inferences about the unfished part of the population as well as the fished part, since the unfished part is the source of most female reproductive output. Even estimates of relative spawning biomass after exploitation, when considered at the population level, will require assumptions or estimates of the spatial distribution of the population across the available habitat, including the distributions of biomass, productivity, and sex ratios.

7. CONCLUSIONS

This study explored modelling approaches used in New Zealand to determine eel stock status, in particular the method used by Graynoth and others (Graynoth et al. 2008; Graynoth & Booker 2009) (GJB), and stock assessment-based approaches (Dunn et al. 2009; Fu et al. 2012). I identified potential improvements in some of the analyses used in the GJB approach, and revised some of these analyses.

My review of the GJB approach found that such GIS-based approaches are reasonable, and that this approach provides a useful foundation for further work. They consider habitat availability, which is appropriate because eels are strongly habitat-dependent, and size patterns, densities, and sex ratios vary substantially at local scales, and mixing rates are low. However, there are problems with the method as originally applied, and some gaps will need additional work. Sex ratio was not considered in the sampling or the models, which is problematic because sex ratios vary markedly between fished and unfished areas, and maintaining female spawning biomass is a primary management objective. The original models did not consider variation between catchments, which my reanalysis indicates is substantial and important. Sampling data are only available for a few catchments, so extending the analysis across New Zealand will require alternative methods and probably additional sampling.

The estimates of original biomass were problematic, because they are based on questionable assumptions about population length structure. I consider the estimates of current biomass to be more reliable and potentially useful.

The GJB method provides a single point estimate of current biomass, not considering changes through time, apart from changes between the original unfished state and the current state. Longfin eels are very long-lived so this approach is reasonable in the short term, but long term monitoring will need to consider temporal effects as well.

The problems for stock assessment modelling of eels include the fractal, highly fragmented and unmixed nature of eel stocks, the high variability of population parameters between locations, and the fact that the fished part of the population will have, on average, different population parameters (sex ratio, density, growth rates) from the unfished part.

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Long-term monitoring of spawning biomass will need to prioritise the unfished areas. Monitoring both the fished and the unfished population requires fishery-independent data, as used in the GJB and Beentjes et al. (in press) approaches. Analyses may use a variety of data inputs, including data from the NZFWDB, site-specific catch data, scientific data, and additional targeted sampling. Sampling is expensive, so should be carefully designed to maximise the precision of management indicators, and to minimize costs. Designing additional sampling may require an appropriate model to be developed first, so that analysts can assess which factors contribute to variability. The modelling approach used will require further development. Models and sample datasets that allow the prediction of sex ratio will also need to be developed.

8. ACKNOWLEDGMENTS

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10. TABLES

Table 1: Models fitted to current biomass, showing percent deviance explained, residual degrees of freedom, the Generalized Cross-Validation statistic (GCV) and the delta-GCV relative to the best model (model 24).

|	Model	% dev expl	Resid df	GCV	Delta GCV
1	1	0.0	211.0	124.01	77.91
2	s(log(LOWFLOW))	36.7	210.0	79.22	33.12
3	s(log(LOWFLOW)) + s(log(SLOPE))	49.0	204.2	67.50	21.40
4	s(LOWFLOW) + s(SLOPE)	49.4	198.1	71.18	25.08
5	s(log(LOWFLOW)) + s(log(SLOPE)) + REGION	54.8	197.9	63.81	17.71
6	te(log(LOWFLOW), log(SLOPE)) + REGION	58.5	191.6	62.40	16.29
7	te(log(LOWFLOW), log(SLOPE))	55.1	196.2	64.47	18.37
8	te(log(LOWFLOW), log(SLOPE)) + LANDCOVER	58.4	193.0	61.64	15.54
9	s(log(LOWFLOW)) + s(log(SLOPE)) + LANDCOVER	54.4	199.0	63.54	17.44
10	s(log(LOWFLOW)) + s(log(SLOPE)) + LANDCOVER + GEOLOGY	58.4	191.6	62.62	16.52
11	s(log(LOWFLOW)) + s(log(SLOPE)) + LANDCOVER + s(ALT)	59.9	190.8	60.81	14.71
12	s(log(LOWFLOW)) + s(log(SLOPE)) + LANDCOVER + s(ALT) + s(STEMP)	62.9	187.3	58.40	12.29
13	s(log(LOWFLOW)) + s(log(SLOPE)) + LANDCOVER + s(STEMP)	59.0	194.7	59.73	13.63
14	s(log(LOWFLOW)) + s(log(SLOPE)) + LANDCOVER + s(ALT) + s(SHADE)	62.5	185.0	60.42	14.31
15	s(log(LOWFLOW)) + s(log(SLOPE)) + LANDCOVER + REGION + s(STEMP)	62.0	190.2	58.08	11.98
16	s(log(LOWFLOW)) + s(log(SLOPE)) + REGION + s(STEMP)	61.5	193.3	56.94	10.83
17	s(log(LOWFLOW)) + s(log(SLOPE)) + RIVER + s(STEMP)	60.9	194.3	57.10	11.00
18	s(log(LOWFLOW), by = RIVER) + s(log(SLOPE)) + RIVER + s(STEMP)	67.3	182.8	53.96	7.86
19	s(log(LOWFLOW), by = RIVER) + s(log(SLOPE), by = RIVER) + RIVER + s(STEMP)	69.9	175.1	54.12	8.01
20	s(log(LOWFLOW), by = RIVER) + s(log(SLOPE), by = RIVER) + RIVER	67.5	175.9	58.07	11.97
21	s(log(LOWFLOW)) + s(log(SLOPE)) + s(DISTSEA) + s(STEMP)	58.7	195.9	59.39	13.29
22	s(log(LOWFLOW), by = RIVER) + s(log(SLOPE), by = RIVER) + s(DISTSEA, by = RIVER)	76.6	167.4	46.15	0.05
23	s(log(LOWFLOW)) + s(DISTSEA, by = RIVER) + s(STEMP)	70.1	184.1	48.67	2.57
24	s(log(LOWFLOW)) + s(log(SLOPE)) + s(DISTSEA, by = RIVER) + s(STEMP)	73.8	177.0	46.10	0.00

Table 2: Models fitted to original biomass, showing percent deviance explained, residual degrees of freedom, the Generalized Cross-Validation statistic (GCV) and the delta-GCV relative to the best model (model 24).

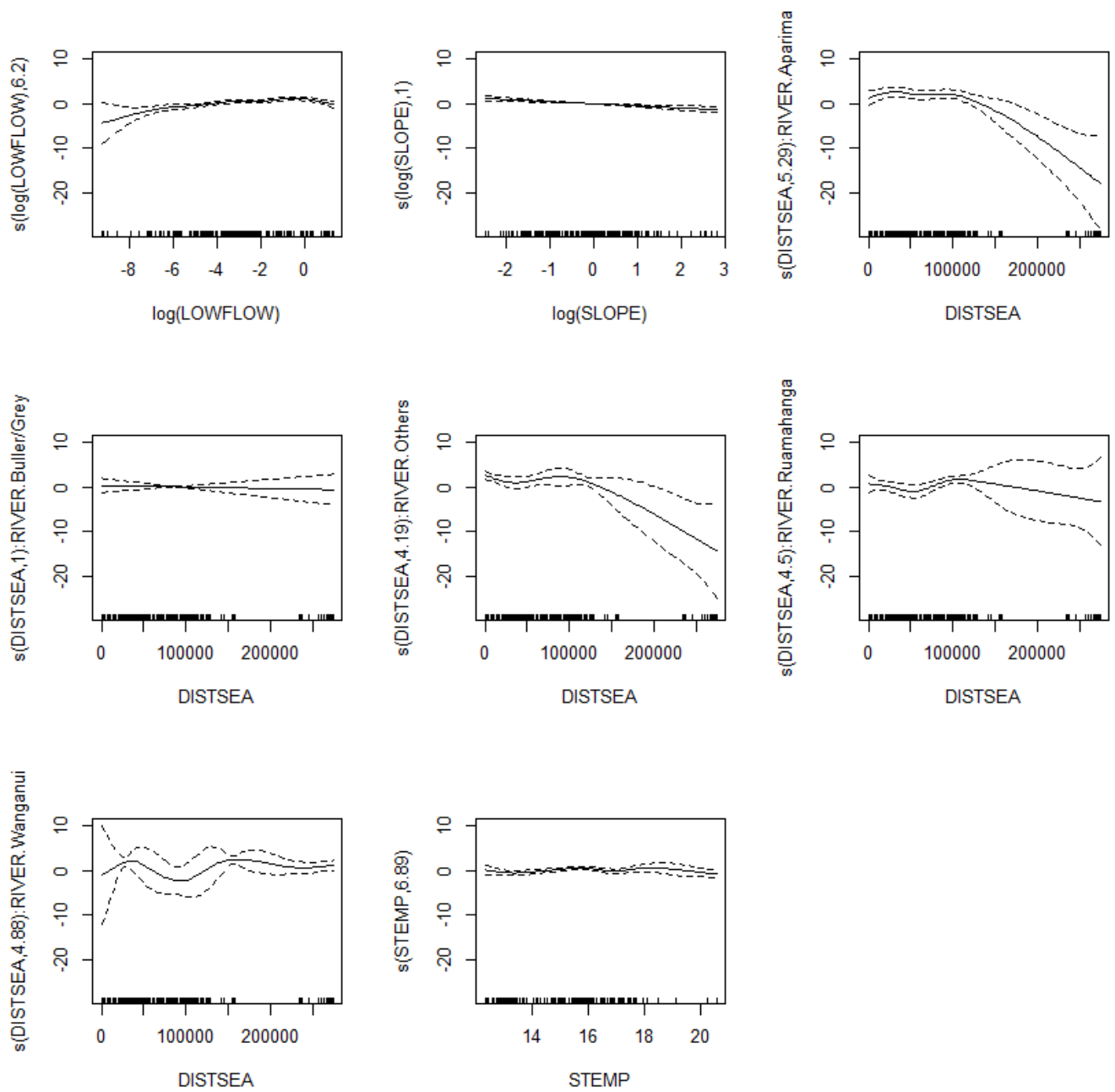|	Model	% dev expl	Resid df	GCV	Delta GCV
1	1	0.0	211.0	210.15	157.0
2	s(log(LOWFLOW))	54.1	205.0	102.21	49.08
3	s(log(LOWFLOW)) + s(log(SLOPE))	62.8	206.5	81.59	28.46
4	s(LOWFLOW) + s(SLOPE)	63.3	200.1	85.71	32.58
5	s(log(LOWFLOW)) + s(log(SLOPE)) + REGION	65.9	202.0	78.19	25.05
6	te(log(LOWFLOW), log(SLOPE)) + REGION	69.7	192.0	76.94	23.81
7	te(log(LOWFLOW), log(SLOPE))	67.0	197.3	79.31	26.17
8	te(log(LOWFLOW), log(SLOPE)) + LANDCOVER	69.2	194.5	76.11	22.97
9	s(log(LOWFLOW)) + s(log(SLOPE)) + LANDCOVER	66.7	200.7	77.32	24.18
10	s(log(LOWFLOW)) + s(log(SLOPE)) + LANDCOVER + GEOLOGY	68.8	194.7	77.14	24.01
11	s(log(LOWFLOW)) + s(log(SLOPE)) + LANDCOVER + s(ALT)	69.9	196.3	73.05	19.92
12	s(log(LOWFLOW)) + s(log(SLOPE)) + LANDCOVER + s(ALT) + s(STEMP)	74.5	187.9	67.54	14.41
13	s(log(LOWFLOW)) + s(log(SLOPE)) + LANDCOVER + s(STEMP)	71.4	195.6	69.91	16.78
14	s(log(LOWFLOW)) + s(log(SLOPE)) + LANDCOVER + s(ALT) + s(SHADE)	73.2	188.3	70.80	17.66
15	s(log(LOWFLOW)) + s(log(SLOPE)) + LANDCOVER + REGION + s(STEMP)	73.7	191.1	67.28	14.15
16	s(log(LOWFLOW)) + s(log(SLOPE)) + REGION + s(STEMP)	73.4	193.2	66.59	13.45
17	s(log(LOWFLOW)) + s(log(SLOPE)) + RIVER + s(STEMP)	72.3	196.5	67.17	14.03
18	s(log(LOWFLOW), by = RIVER) + s(log(SLOPE)) + RIVER + s(STEMP)	76.9	183.3	64.35	11.22
19	s(log(LOWFLOW), by = RIVER) + s(log(SLOPE), by = RIVER) + RIVER + s(STEMP)	75.6	185.2	66.57	13.44
20	s(log(LOWFLOW), by = RIVER) + s(log(SLOPE), by = RIVER) + RIVER	73.6	189.3	68.78	15.65
21	s(log(LOWFLOW)) + s(log(SLOPE)) + s(DISTSEA) + s(STEMP)	71.1	190.0	74.81	21.68
22	s(log(LOWFLOW), by = RIVER) + s(log(SLOPE), by = RIVER) + s(DISTSEA, by = RIVER)	83.7	168.8	53.67	0.54
23	s(log(LOWFLOW)) + s(DISTSEA, by = RIVER) + s(STEMP)	79.9	179.0	58.59	5.46
24	s(log(LOWFLOW)) + s(log(SLOPE)) + s(DISTSEA, by = RIVER) + s(STEMP)	82.4	175.9	53.13	0.00

11. FIGURES
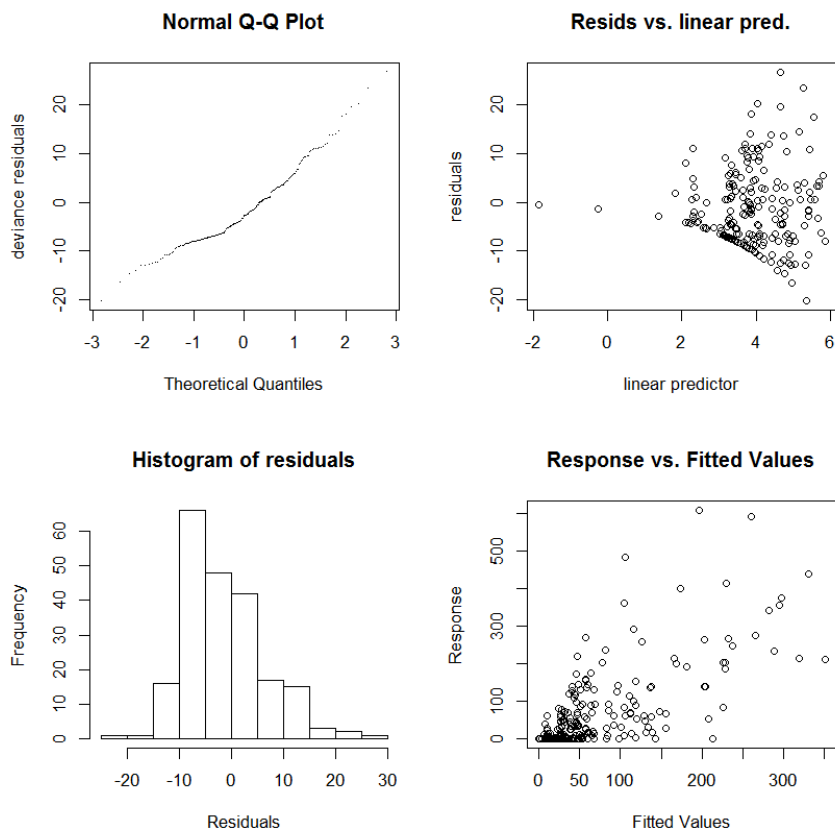
Figure 1: Diagnostic plots for the model of current biomass as a function of flow and slope, as applied by GJB.
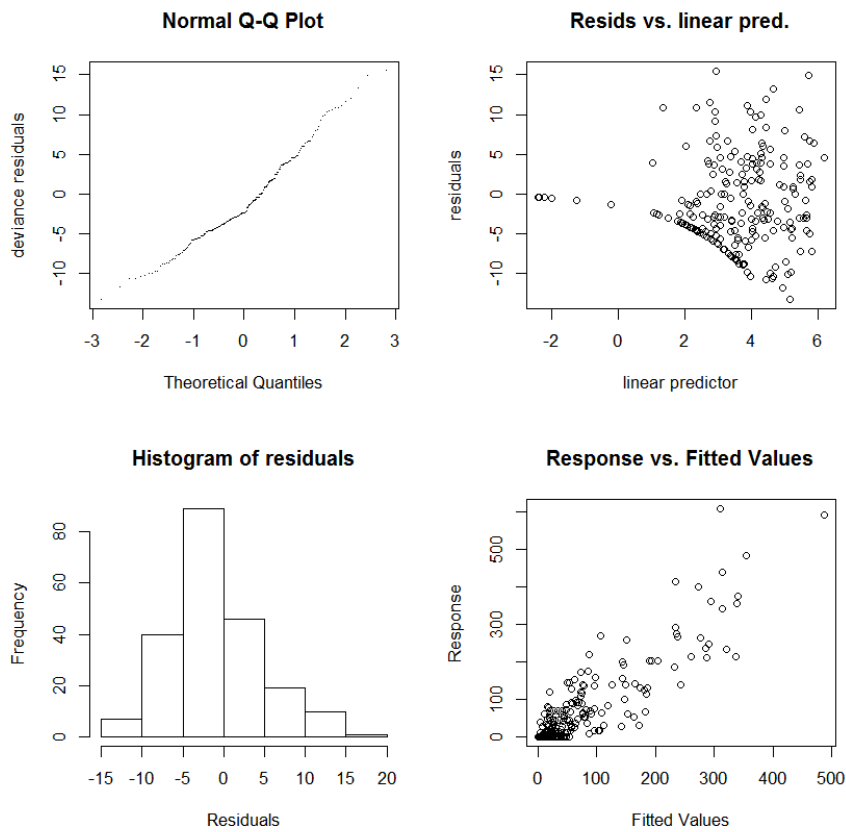
Figure 2: Diagnostic plots for the model of current biomass as a function of log(flow), log(slope), temperature, and distance from the sea by catchment (river).

Figure 3: Predicted response of current biomass as a function of smoothed effects of flow, slope, temperature, and distance from the sea by catchment (river).