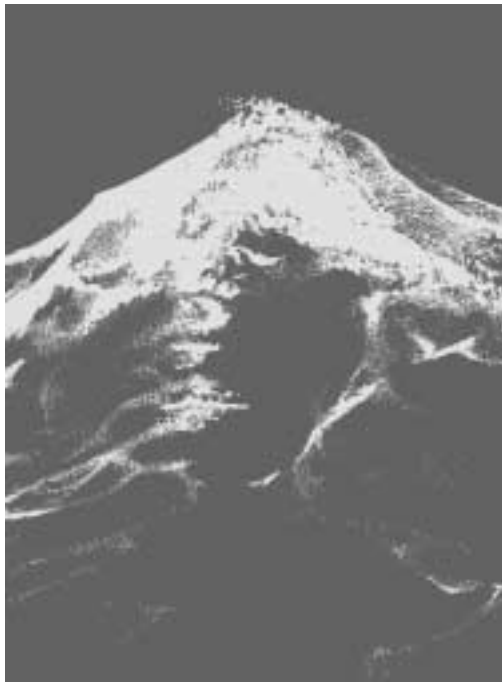


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Longfin eels need reserves: modelling the effects of commercial harvest on stocks of New Zealand eels

Simon D. Hoyle^{A,B,D} and Don J. Jellyman^C

^AQueensland Department of Primary Industries, Southern Fisheries Centre, PO Box 76, Deception Bay, Qld 4508, Australia.

^BSchool of Mathematical Sciences, Queensland University of Technology, GPO Box 2434, Brisbane, Qld 4001 Australia.

^CNational Institute of Water and Atmospheric Research Ltd, Box 8602 Christchurch, New Zealand.

^DCorresponding author; simon.hoyle@dpi.qld.gov.au

Abstract. Freshwater eels in New Zealand are heavily exploited by the commercial fishery and, to a lesser extent, by customary fisheries. A model was developed to investigate the effect of the New Zealand commercial eel fishery on escapement of migrating longfin (*Anguilla dieffenbachii*) and shortfin (*A. australis*) eels. Exploitation rates of 5% and 10% per year reduced the spawning per recruit of *A. dieffenbachii* females by 83% and 96.5%, respectively, below unexploited levels. The model suggests that New Zealand longfin eels may be severely recruitment overfished and only absence of fishing in some productive areas is likely to be effective in maintaining at least 50% of spawning per recruit. Being younger at spawning, eels are less susceptible to overfishing. Using the current minimum legal weight (220 g), the spawning per recruit of *A. australis* females was reduced by only 48% at an exploitation rate of 10% per year.

Introduction

The complex life history of eels involves a marine larval phase (leptocephalus), metamorphosis in estuaries (glass eel), development of pigmentation and growth in fresh water for between 5 and 100 years (elver to adult/yellow eel), followed by sexual maturation (silver eel) and migration to the sea to breed. In the various international fisheries, exploitation can take place at any or all of these post-larval stages. In New Zealand, exploitation is mainly confined to the yellow eel stage.

In eel species with extensive recruitment data (*Anguilla japonica*, *A. anguilla*, *A. rostrata*), the numbers of migrating glass eels (juveniles recruiting to fresh water from the sea) have declined greatly in recent years (Gascuel 1987; Moriarty 1990; Dutil *et al.* 1989; Castonguay *et al.* 1994). Suggested causes of these declines include commercial fishing of elvers and glass eels, overfishing of adult stocks, chemical contamination, habitat modification (such as construction of in-stream barriers), oceanic changes and episodes of disease or parasites (Castonguay *et al.* 1994).

It is clear that egg production per recruit, or spawning per recruit, is vulnerable to exploitation of the adult stock, since eels breed only once and at a relatively advanced age. Unlike most other species, eels contribute to either spawning or fishing yield, but never to both. Female age at spawning

varies between species and locations, ranging from a mean age of 7.9 years for *A. anguilla* in the Imsa river, Norway (Vøllestad and Jonsson 1988), to 93 years for *A. dieffenbachii* in the subalpine Lake Rotoiti, New Zealand (Jellyman 1995). In an area of New Zealand with better conditions, *A. dieffenbachii* females were observed to mature between the ages of 25 and 60 years (Todd 1980). In the same locations, migrating female *A. australis* ranged from 10 to 35 years (Todd 1980).

Late-maturing species are especially vulnerable to overfishing. For example, maturity at over 18 years is a common trait of species at significant risk of extinction, including *A. rostrata*, in the Great Lakes–St Lawrence biozone (Parent and Schriml 1995). Concern has been expressed about the effect of fishing on the number of New Zealand longfin eel spawning females (Chisnall and Hicks 1993; Jellyman 1995), however, the magnitude of the effect of fishing on egg production is often not clearly understood, since reductions in numbers of migrating eels may not be apparent.

Reductions in egg production are a normal consequence of exploitation and at moderate levels, are not usually a problem. The key is to maintain egg production above the level where successive generations may replace each other. Exploitation beyond this level is one definition of recruitment overfishing (Sissenwine and Shepherd 1987).

The appropriate level varies between taxa and populations and through time, but has not been determined for any eel species. Studies of a range of European and North American fish stocks have identified a conservative level of 30% of unfished spawning per recruit, at which level, 80% of studied stocks were able to replace themselves (Mace and Sissenwine 1993). However, the unusual life history of eels makes the appropriateness of this estimate very uncertain. Since eels may enter the adult fishery many years after the glass eels initially recruit to streams, reduced recruitment only affects the adult fishery after a long period. Thus slow-growing adult eel fisheries can maintain high fishing yields for significant periods of time while egg production becomes greatly diminished. In sounding a note of caution about exploitation of New Zealand eels, Castle (1972) likened such a scenario to 'drawing on one's capital as opposed to receiving annual interest'.

The New Zealand eel fishery targets the yellow (feeding) eel stage of two main species, the longfin (*Anguilla dieffenbachii*) and shortfin eel (*A. australis*), throughout both the North and South Islands. Doubts have been expressed about the sustainability of the *A. dieffenbachii* component of the fishery, with evidence of a substantial decline in recruitment (Jellyman *et al.* 2000; Glova *et al.* 2001). Management of the fishery is currently under review, with the South Island fishery moving to a quota system on 1 October 2000, but there is continuing debate over appropriate methods of management and levels of fishing pressure.

Eels have high value both to local economies and as a culturally significant food for the Maori people. Large female *A. dieffenbachii* are particularly valuable as a cultural food, as well as for their contribution to spawning. It is a challenge for fishery managers to maintain the long-term economic value of a fishery in which the components respond so differently to fishing pressure.

In this study, we used a simulation model to estimate the effect of fishing on the spawning per recruit of New Zealand eels and on fishing yield per recruit and compared the impacts of various management measures. The management regimes we investigated relate to those already in practice in New Zealand: minimum (220 g for both species) and maximum legal weights (4000 g for *A. dieffenbachii* in the South Island). Maximum legal weights allow large females, the most important reproductive individuals, to escape.

We also examined the effect of various exploitation rates, including zero exploitation in closed areas. The panmictic nature of eel populations gives closures particular power, since recruitment sourced from the reserve is distributed throughout the species' range. The long-term (equilibrium) effect of area closures is estimated, very simply, by considering the effect of returning a proportion of the fishery's production to an unfished state. Since all estimates in this study are made relative to this unfished state, modelling is unnecessary.

Until recently, population models of anguillid fisheries have focused on maximizing fishing yield using either a yield per recruit approach (Gascuel and Fontenelle 1994), or a more sophisticated demographic modelling approach (De Leo and Gatto 1995, 1996). Dekker (2000) addressed the effect of fishing on spawning of *A. anguilla* in a heavily exploited fishery, Lake IJsselmeer in the Netherlands. To model the impact of commercial harvest on adult eel escapement and fishing yield, we adapted Francis and Jellyman's (1999) model, which was designed to look at the ability of length monitoring to detect changes in the exploitation rate of the commercial fishery. We hypothesized that the impact of commercial fishing would be considerably greater for *A. dieffenbachii* than for *A. australis* and that even moderate levels of exploitation of *A. dieffenbachii* was unlikely to be sustainable.

Methods

The model essentially takes a per-recruit approach. It incorporates variation in growth and initial length among individual eels by modelling twenty growth-rate classes, with growth rates ranging from slow to fast across a normal distribution. It models maturity using the approach of de Leo and Gatto (1995). As we are concerned with long-term effects of management strategies, rather than uncertainty or short-term responses, we do not model stochasticity in recruitment or model more than one cohort. *Anguilla australis* males seldom exceed the minimum legal weight of 220 g and this effectively excludes them from the model.

The data largely come from Francis and Jellyman (1999), who synthesized three sources: (i) the 1995–96 and 1996–97 data gathered in processing sheds for the main fisheries; (ii) the New Zealand National Institute of Water and Atmosphere Research (NIWA) Freshwater Eel Database, which holds information on almost 40 000 eels gathered from various sampling programs between 1974 and 1998; and (iii) published information for New Zealand eels and other freshwater eel species. The New Zealand eel fishery uses fyke nets almost exclusively.

Basic assumptions

The probability that an eel of length L will become mature (μ_L) is calculated using the equation from de Leo and Gatto (1995):

$$\mu_L = \frac{\gamma}{1 + \exp\left(\frac{\lambda - L}{\eta}\right)} \quad (1)$$

where γ is the maximum rate of metamorphosis, λ is a semi-saturation constant and η is inversely proportional to the slope of the metamorphosis curve at $L = \lambda$. Parameters for the model are those described by Francis and Jellyman (1999) (Table 1).

We also use Francis and Jellyman's maturity parameters for *A. australis* (Table 2). Our maturity parameters for *A. dieffenbachii* were estimated using the procedure they described for *A. australis*, based on length at maturity data from Lake Ellesmere (Te Waihora) (Todd 1980). Age at maturity data was not used because samples were either missing or insufficient.

Estimates of total mortality (Z) range from 0.01 to 0.05 for *A. dieffenbachii* in unfished or lightly fished areas and 0.02 to 0.25 for *A. australis* in unfished and heavily fished areas (B. L. Chisnall and

Table 1. Model parameters for both sexes and for both species unless stated otherwise
After Francis and Jellyman (1999) and Todd (1981).

Type	Parameter	Longfin eel (<i>A. dieffenbachii</i>)	Shortfin eel (<i>A. anguilla</i>)
Growth	<i>a</i> ₁	8.1 cm	8.1 cm
	<i>a</i> ₂	1.2 cm year ⁻¹	1.2 cm year ⁻¹
	<i>b</i> ₁	2.42 cm	2.42 cm
	<i>b</i> ₂	0.34 cm ⁻¹	0.34 cm ⁻¹
Length–weight	–	1.18 × 10 ⁻³	1.48 × 10 ⁻³
	β	3.18	3.08
Length fecundity	<i>c</i>	5.93	3.87
	<i>d</i>	4.19	3.51
Natural mortality	<i>M</i>	0.04 year ⁻¹	0.04 year ⁻¹

R. T. T. Stephens, unpublished data; Jellyman *et al.* 1995). Estimates of the natural mortality rate (*M*) for unfished populations were 0.038 and 0.036 for *A. australis* and *A. dieffenbachii*, respectively, in a small coastal lake and 0.042 for *A. dieffenbachii* in a cool, high-country lake (Jellyman 1995; Jellyman *et al.* 1995; Horn 1996). Some of these estimates were based on relatively small samples and all were based on catch curves. We have set *M* to 0.04 years⁻¹ for all age classes, both sexes and both species (see Table 1). Exploitation rate is assumed to average about 0.1, but is quite uncertain and clearly varies considerably between areas. The length *L* of an eel of age *i* is calculated by:

$$L = a_1 + b_1i + (a_2 + b_2i)\epsilon \tag{2}$$

where the parameters (*a*₁, and *b*₁) define mean length as a linear function of age, (*a*₂, and *b*₂) describe the standard deviation of length-at-age and ϵ is a standard normal variate representing between-individual variation in length at age (Francis and Jellyman 1999). Parameters for this equation are given by Francis and Jellyman (1999). The twenty values of ϵ used to define the growth classes were the *j*/40 quantiles of the standard normal distribution, where *j* = 1,3,5,...,39. Linear growth is a characteristic of New Zealand eels and has been observed for other eel species (Jellyman 1997 and references therein). Jellyman (1995) has suggested that lack of investment in annual spawning leads to linear growth. Weight is calculated by $W = \alpha L^\beta$. Exploitation rate (*E*_{*L*}) at length *L* is calculated using Equation 3:

$$E_L = a + b(L - L_{\text{MinLW}})$$

if minimum legal weight < *L* < maximum legal weight, otherwise:

$$E_L = 0 \tag{3}$$

where *a* and *b* are the intercept and slope of the size-selectivity function. The size selectivity of the fishery overall has not been

estimated, so a flat selectivity curve was assumed. However, the sensitivity of this assumption was also investigated.

The number of eggs in metamorphosed eels is calculated using the equation:

$$G_L = cL^d$$

where *c* and *d* are the parameters of the length–fecundity equation for the species (Table 2). The cohort of eels is followed from the age of one, when both maturity and exploitation are minimal, to age 100, when insignificant numbers remain.

Demographic model

Given the number *N*_{*i,c*} of yellow pre-reproductive eels at age *i* in growth class *c*, we compute, in the following order.

(i) Eel length *L*_{*i,c*} by using Eq. 2, eel weight *W*_{*i,c*} at length *L*_{*i,c*} and number of eggs *G*_{*i,c*} at length *L*_{*i,c*} assuming metamorphosis.

(ii) Number of eels undergoing metamorphosis at age *i* in growth class *c*:

$$M_{i,c} = \mu_L N_{i,c}$$

number of eels remaining after metamorphosis:

$$N^*_{i,c} = (1 - \mu_L) N_{i,c}$$

(iii) Number of eels surviving natural mortality:

$$N^{+}_{i,c} = (1 - e^{-M}) N^*_{i,c}$$

(iv) Number of eels harvested at age *i* in growth class *c*, given *E*_{*L*}, the exploitation rate at length:

$$Y_{i,c} = E_L N^{+}_{i,c}$$

number of eels escaping fishing and making up the following year's yellow eel stock:

$$N_{i+1,c} = (1 - E_L) N^{+}_{i,c}$$

Thus

$$N_{i+1,c} = N_{i,c} (1 - \mu_L) \cdot e^{-M} \cdot (1 - E_L) \quad (i = 1, 2, \dots, i_{\text{max}}, c = 1, 2, \dots, c_{\text{max}})$$

The overall yield is thus given by the contribution by all age classes and growth classes of legal weight, namely:

$$Y^{\#} = \sum Y_{i,c} \quad (i = 1, 2, \dots, i_{\text{max}}, c = 1, 2, \dots, c_{\text{max}})$$

while overall biomass is:

$$W^{\#} = \sum W_{i,c} Y_{i,c} \quad (i = 1, 2, \dots, i_{\text{max}}, c = 1, 2, \dots, c_{\text{max}})$$

Table 2. Estimated values of the maturity parameters for eels in Lake Ellesmere
Shortfin parameter values come from Francis and Jellyman (1999).

Type	Parameter	Longfin female (<i>A. dieffenbachii</i>)	Longfin male (<i>A. dieffenbachii</i>)	Shortfin female (<i>A. australis</i>)
Maturity	γ (no units)	0.1	0.34	0.25
	λ (cm)	107.7	62.0	54.6
	η (cm)	5.58	2.43	2.8

Metamorphosing biomass is:

$$MB^{\#} = \sum W_{i,c} M_{i,c} \quad (i = 1, 2, \dots, i_{max}, c = 1, 2, \dots, c_{max})$$

Eggs in metamorphosing eels are:

$$G^{\#} = \sum G_{i,c} M_{i,c} \quad (i = 1, 2, \dots, i_{max}, c = 1, 2, \dots, c_{max})$$

Decision variables

Any management policy simulated by the model is defined by a combination of (i) fishing mortality, (ii) minimum legal weight and (iii) maximum legal weight. The model is used to investigate the effect of management alternatives for *A. australis* and *A. dieffenbachii* fisheries on relative spawning per recruit and relative yield per recruit. The word ‘relative’ is used because performance can only be assessed against the unexploited population. We do not know either total biomass or total egg production, or even total equilibrium yield, since the natural population is not at equilibrium.

We examined the effect of the following management measures, various rates of exploitation, minimum legal weight of 150 g or 220 g and maximum legal weights ranging between 220 g and 4000 g. For each component of the eel fishery, we estimated the minimum legal weight that would maximize yield per recruit at a range of exploitation rates and the exploitation rate that would maximize yield per recruit at the current minimum legal weight (220 g).

We also investigated the sensitivity of the results for *A. dieffenbachii* females to two alternative selectivity functions, since it is possible that catchability of eels in the fyke nets used in the fishery increases with size, as asserted by eel fishers. In the standard (no size selectivity) model, the selectivity intercept variable *a* is set to 0.05, with *b* = 0. For the alternative selectivity, we assumed that catchability was proportional to length, on the assumption that larger eels are behaviourally dominant and are more likely to encounter fishing gear. We investigated the way this assumption affected spawning per recruit and estimates of *E*, when calculated from the catch of the more abundant smaller eels. In this model, *a* is set to 0.02 and *b* is adjusted so that the average exploitation rate for ages 26 to 45 is the same as observed when *a* = 0.05 and *b* = 0.

Results

Anguilla australis females

The models predicted a 48% reduction in spawning per recruit at the current minimum legal weight of 220 g, with an annual exploitation rate of 10%, compared with the unexploited situation (Fig. 1a). Reduction of spawning per recruit increased to 59% at a minimum legal weight of 150 g.

Yield was also affected by minimum legal weight, but only marginally. The current minimum legal weight reduced yield per recruit by about 10% from a 150 g minimum legal weight, assuming an exploitation rate of 10% (Fig. 1b). At higher exploitation rates the optimum minimum legal weight increased (Fig. 1c).

Anguilla dieffenbachii females

At the current minimum legal weight of 220 g, the predicted spawning per recruit was reduced by 83% and 96.5% from unexploited levels at annual exploitation rates of 5% and 10% respectively. There was a greater reduction in spawning per recruit with a 150 g minimum legal weight, where reductions

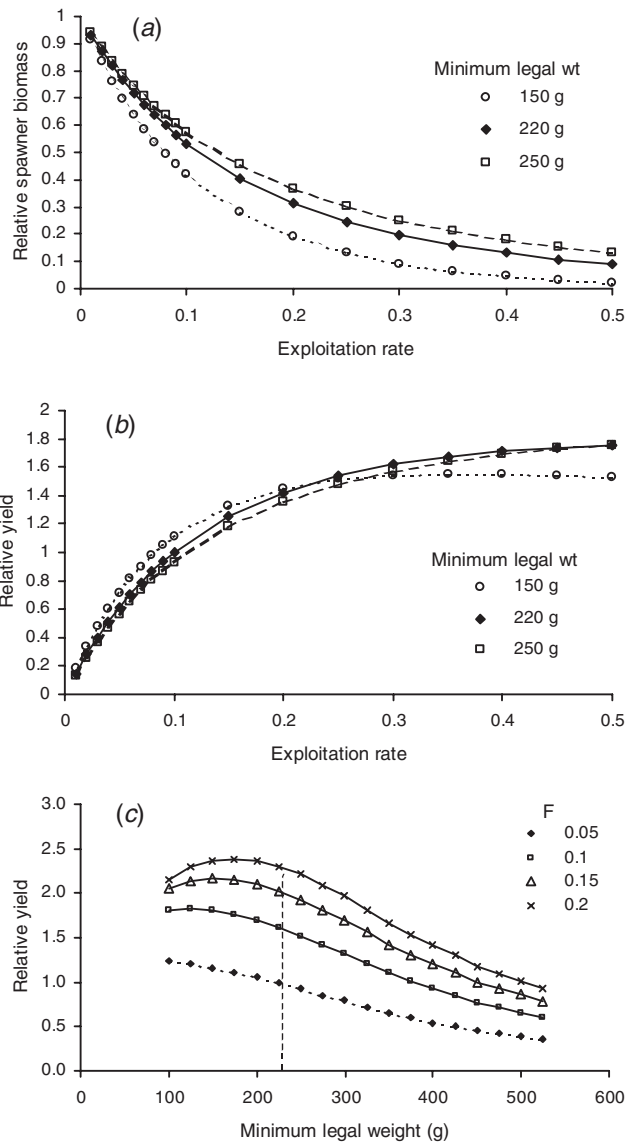


Fig. 1. Female *A. australis* at equilibrium. Relative spawning per recruit and yield per recruit at a range of exploitation rates and minimum legal weights: (a) relative spawning per recruit (the decline in relative spawning per recruit of female *A. australis* with increasing fishing pressure is moderated by the current minimum legal weight of 220 g; (b) relative yield per recruit increases with exploitation rate for all minimum legal weights (minimum legal weight has a relatively small effect on yield per recruit except at high fishing pressures; and (c) relative yield per recruit at a range of minimum legal weights and exploitation rates.

were 84% and 97.2% respectively (Fig. 2a). At alternative minimum legal weights of 800 g and 1250 g, the spawning per recruit was less affected by exploitation.

The optimum yield per recruit at the current minimum legal weight was obtained with a relatively low exploitation rate of between 5% and 8%. However, raising the minimum legal weight increased yield at these exploitation levels. The

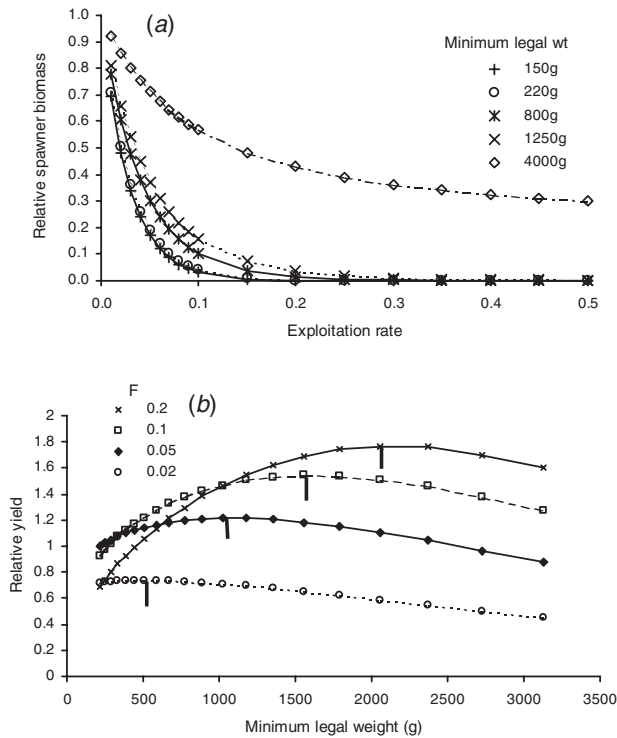


Fig. 2. Female *A. dieffenbachii* at equilibrium. Relative spawning per recruit and yield per recruit at a range of minimum legal weights and exploitation rates for female *A. dieffenbachii*: (a) relative spawning per recruit; and (b) relative yield per recruit. Maxima for each exploitation rate are marked with drop-down lines.

optimum minimum legal weight increased as the exploitation rate increased (Fig. 2b). At an exploitation rate of 5%, the optimum minimum legal weight was 1100 g, which increased yield per recruit by 21%. At an exploitation rate of 10%, the optimum minimum legal weight was 1600 g, increasing yield per recruit by 55%.

The present maximum legal weight of 4000 g in the South Island slightly increased spawning per recruit beyond that without a maximum legal weight. At exploitation rates of 5% and 10%, the imposition of this maximum legal weight increased spawning per recruit by factors of 1.5 and 1.9 respectively. Substantial increases in spawning per recruit were only predicted when maximum legal weight was reduced to 2000 g or less (Fig. 3a). However, such a reduction in maximum legal weight also considerably reduced yield per recruit (Fig. 3b).

When the size-selectivity function was fitted to the data using Equation 3, the variable *b* was estimated as 0.00191. If this form of size selectivity occurred in the fishery, spawning per recruit would be reduced by 94.7% from the unfished state, as opposed to 83% for the non-size selected scenario.

Anguilla dieffenbachii males

Predicted rates of migration per recruit and yield per recruit of male *A. dieffenbachii* and female *A. australis* responded to

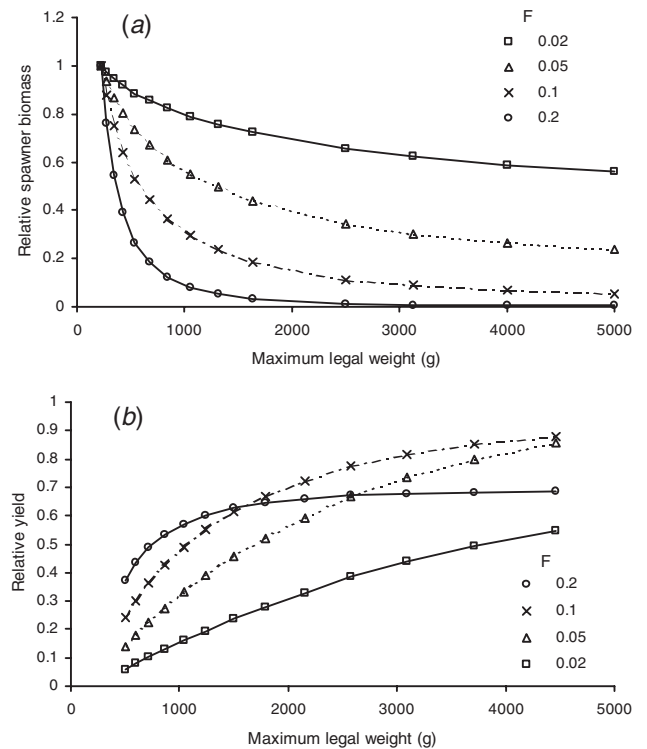


Fig. 3. Female *A. dieffenbachii* at equilibrium. Relative spawning per recruit and yield per recruit by exploitation rate and maximum legal weight: (a) relative spawning per recruit (maximum legal weight does little to increase relative spawning per recruit until it is 2000 g or less; and (b) relative yield per recruit. All curves tend towards 1, the yield per recruit without a maximum legal weight for the indicated exploitation rate.

exploitation in a similar way, since their growth rate, mortality and length at migration is similar. Increasing the minimum legal weight did not increase the yield of male *A. dieffenbachii*, unless exploitation rate was 14% or more. At an exploitation rate of 5%, a minimum legal weight of 800 g lowered yield per recruit by 84% compared with the current legal size and at an exploitation rate of 10%, a minimum legal weight of 1250 g lowered yield per recruit by 95.5%.

At the current minimum legal weight, the maximum yield was obtained at a high 32% annual exploitation rate. Maximum legal weight had no significant effect on yield of male *A. dieffenbachii*. Thus the male and female components of the *A. dieffenbachii* fishery respond very differently to exploitation.

Discussion

The model used here predicts that current levels of fishing will seriously affect the sustainability of the New Zealand longfin eel fishery. This prediction seems to be borne out by the present rarity of large eels in the fishery (Beentjes and Chisnall 1997; Beentjes 1999) and by observed declines in recruitment in some areas (NIWA, unpublished data). The model implies that *A. dieffenbachii* recruitment is likely to

have been reduced considerably more than *A. australis* recruitment. This is consistent with a comparison of the age and size structure of the *A. dieffenbachii* and *A. australis* populations (Beentjes and Chisnall 1998; Beentjes 1999).

Managing to ensure adequate spawning stock

Estimates of spawning stock biomass have not been attempted for *A. dieffenbachia*, but given the longevity of the species, management should be conservative (Jellyman 1995). Our models suggest that the existing yellow eel fishery will remove the great majority of *A. dieffenbachii* females before they can spawn, despite the lack of a fishery targeting migrating eels (with the exception of the Lake Ellesmere fishery for migratory *A. australis* males).

Eels can be recruitment overfished without being growth overfished and without yield decreasing noticeably in the medium term. Low recruitment takes a long time to affect yield, since recruits do not enter the fishery until between 14 and 24 years. By this stage, a similar period may be required for recovery to begin.

We cannot know exactly what proportion of the unfished egg production is required to maintain sufficient recruitment. This question has been addressed for a range of stocks, with the conclusion that where there is no basis for estimating the replacement level of spawning per recruit, 30% of the unfished level is a conservative default value (Mace and Sissenwine 1993). Given the current depleted state of the *A. dieffenbachii* fishery, a more conservative level, such as 50% of unfished spawning per recruit (in Jellyman (1993) with respect to escapement of migrating *A. dieffenbachii* females), may be justified. Three mechanisms to attain such goals are considered in the light of the modelling results already presented. The mechanisms are: the imposition of legal weights (minimum and maximum); control of exploitation rate; and long-term spatial closures.

Minimum legal weight

The vulnerability of *A. dieffenbachii*, especially in the years before they reach maturity, is of particular concern. A minimum legal weight that would protect significant numbers of female *A. dieffenbachii* spawners would exceed the length at migration of all *A. australis* and male *A. dieffenbachii*, which would therefore be lost to the fishery. The current minimum legal weight of 220 g allows significant numbers of female *A. australis* to survive to migration, they reach a 1% annual migration rate at the weight of 190 g, increasing to 2% at 220 g and 20% by 420 g. However, female *A. dieffenbachii* spawners only reach a 1% migration rate at a weight of 2300 g and the model predicts that few survive the fishery to reach this length. It is not practical to have a different minimum legal weight for *A. australis* and *A. dieffenbachia*, or for the different sexes, for both administrative and enforcement reasons and because fishing equipment does not distinguish between the species.

Maximum legal weight

The principle behind the maximum legal weight of 4000 g for *A. dieffenbachii* is to allow 50% escapement of migrating eels (Jellyman 1993). Because fecundity increases as length to the power of 4.2 (Todd 1981), larger eels would represent a much higher proportion of egg production.

Maximum legal weight has potential to protect *A. dieffenbachii* females effectively, but to do so it would have to be set much lower than the present 4000 g. A more suitable level may be 2 kg, but this requires further analysis with data on catchability by size. However, there are practical obstacles to such a management measure. If, as is probable, catchability increases with size, large *A. dieffenbachii* would be caught frequently with attendant likelihood of handling mortality. In addition, a narrow window of catchable lengths would give fishers an economic incentive to fish harder within the window, to catch eels before they grow beyond the weight limit. This would reduce the efficiency of the fishery and still result in few eels reaching maturity.

Control of exploitation rate

A lowered exploitation rate could be used to increase the escapement of female *A. dieffenbachii* spawners, but a meaningful increase would require a substantial reduction throughout the fishery. Our models have demonstrated that spawning per recruit of *A. dieffenbachii* females would reach 50% of unfished levels at a long-term exploitation rate of approximately 2%. A quota system could be used to manage the exploitation rate. However, such a large reduction in exploitation rate would severely reduce the catch of *A. australis* and male *A. dieffenbachii*. As we discuss below, those components of the fishery would actually yield better at higher exploitation rates.

Unfished areas

Closed areas are currently attracting much attention in fisheries management and in New Zealand date back to the traditional Maori concept of 'rahui' (temporary or permanent closures) that applied to both marine and fresh waters. Modelling suggests that marine reserves are most useful for species that remain within reserve boundaries and have abundant larval spillover (Sladek Nowlis and Roberts 1999; Sladek Nowlis 2000). Reserves can help guarantee the sustainability of a fishery, even when fishing mortality outside the reserve cannot be well controlled (Mangel 2000) and total stock size is highly uncertain (Walters 2000). Eel biology fits the former criteria well, with their panmixis, territoriality and subdivision into catchments and the latter criteria of uncertain stock size and fishing mortality rate are also true.

At present exploitation rates, our models suggest that the fishery may be removing the great majority of *A. dieffenbachii* female migrants from accessible waters. Thus, most egg production must come from eels from unfished areas. The most appropriate way of ensuring adequate escapement of

migrants may be to establish and maintain unfished areas (Jellyman 1993, 1995). The alternative of protecting females in fished areas is not practical for the reasons outlined above.

Given the low contribution of fished areas, currently unfished areas must be greatly increased to achieve even 30% of unfished spawning per recruit, a conclusion also reached by Jellyman (1993). Areas where growth rates are high, *A. dieffenbachii* dominate and most eels are female, would be the most appropriate areas for closure.

Most currently unfished areas are within national parks and most of these are well inland at high altitudes, where productivity of migratory eels can be expected to be low. For example, the average generation time for female eels in Lake Rotoiti, Nelson Lakes National Park, is 93 years (Jellyman 1995), so it is likely they make a relatively small contribution to egg production. All of the North Island lakes and three-quarters of the area of the South Island lakes within national parks are affected by hydroelectric dams (Jellyman 1998), and would have associated recruitment and downstream passage problems.

Managing to optimise yield

Setting aside large productive areas to allow *A. dieffenbachii* egg production to recover represents a significant short-term cost to the fishery. However, if sufficient areas are set aside to guarantee egg production, the remaining areas can be managed to maximize fishing yield. Because species composition, sex ratio and growth rate varies among areas, management must also vary among areas if it is to optimise yield.

Minimum legal weight

Improvement of yield in the long term could theoretically be achieved by increasing the weight at which female *A. dieffenbachii* are taken. This would be impractical to achieve with regulations, because the ideal minimum weight to maximize yield depends on the sex ratio and species composition of the area and the fishing gear does not distinguish between species or sexes.

Exploitation rate

At the current minimum legal weight, the best yield from female *A. dieffenbachii* would be obtained with a comparatively low exploitation rate, between 5% and 8%. Low exploitation rate allows female *A. dieffenbachii* to reach larger sizes, at which weight gain is most rapid given a linear growth trajectory. On the other hand, the yields of male *A. dieffenbachii* and female *A. australis* tend to increase under greater fishing pressure. Therefore the appropriate exploitation rate depends on the sex ratio and species composition of a particular population within the fishery.

Management at finer scales

The species ratio, the sex ratio and the future sex ratio of the undifferentiated eels vary between areas at all scales,

with differences between the North and South Islands and between habitat types within streams. Individual fishers could maximize their own yield by adjusting fishing pressure and minimum weight to the areas in which they fish. The appropriate weight limit and fishing pressure would depend on the species and sex composition of the area. Management by individuals, by giving individuals exclusive access to areas, would facilitate competition between individuals in an area, driving them to catch smaller eels and reducing the efficiency of the fishery.

Uncertainty in fishing mortality estimates

Unfortunately, there is reason to suspect that the spawning per recruit predicted by this modelling exercise is overly optimistic. If large eels are indeed more catchable (using fyke nets) than small eels, the current exploitation rate has probably been underestimated. This is for two reasons. Firstly, selectivity that increases with size strongly biases the catch curve towards a shallower slope. In other words, the fishery catches a disproportionate (though still very low due to their rarity) number of larger, older fish, so the age structure of the catch curve is flatter than the age structure of the population. Thus total mortality estimated from the catch curve underestimates the total mortality of the population. Similar effects may occur when mortality rates are estimated from electrofishing data, which can also be size selective (Anderson 1995). Secondly, since there are usually too few individuals in the large size classes to influence total mortality estimates (e.g. Jellyman *et al.* 1995), the higher exploitation rate of larger animals will not be included.

If exploitation rate is higher than we have assumed, then spawner numbers are affected more severely than we have estimated. Counterbalancing this is a potential upward bias on estimates of exploitation rate. Owing to the high variability of eel growth rates and lengths at migration, a catch curve will include losses due to migration as well as those due to fishing. Size selectivity may also lead to slight overestimates in the ratios of females to males and the ratio of *A. dieffenbachii* to *A. australis*.

Assumptions and model structure

As with any modelling exercise, there are a number of uncertainties to do with parameter estimates and the type of model used. The most important unknown variable in this analysis is the size selectivity of the fishery. Larger eels are ecologically dominant (Chisnall and Hicks 1993) and probably have a larger home range than smaller eels, so are more likely to encounter fishing gear. In addition, since the larger eels are more valuable than smaller eels, fishers have preferentially targeted them. Estimating this selectivity function would improve the predictions of the model and, as discussed above, would reduce the estimates of spawning per recruit.

It is difficult to ascertain the influence of eel density on growth, sex differentiation and maturation, but density is

likely to be important in determining both yield and egg production (Horn 1996; Vøllestad and Jonsson 1988). Sex determination of eels is influenced environmentally and is likely to be affected by density (Colombo and Grandi 1996; Beullens *et al.* 1997), with males tending to be more common at higher densities (Krueger and Oliveira 1999). Size distribution may complicate density effects, since eels change diet as they grow (Ryan 1986; Jellyman 1989; Sagar and Glova 1998) and different size classes may not compete with one another. Large piscivorous *A. dieffenbachii* may reduce the densities of fish, such as bullies (*Gobiomorphus cotidianus*), that compete with smaller *A. dieffenbachii* and *A. australis*, but they are also cannibalistic (Jellyman 1989) and their presence influences the distribution of smaller eels of both species (Chisnall and Hicks 1993).

'Compounding' effects occur when reduced recruitment begins to affect the number of adults and compounds the direct impact of fishing pressure on spawning per recruit. Although, as modelled, *A. australis* spawning per recruit is less affected by fishing pressure than that of *A. dieffenbachii*, the time scale of compounding would be shorter because *A. australis* migrate at a younger age. Thus, given reduced recruitment, *A. australis* are likely to decline (and subsequently recover) more quickly than *A. dieffenbachii*. *Anguilla dieffenbachii* may be more resistant than *A. australis* to medium-term recruitment collapses but more vulnerable to long-term increases in adult mortality rate.

A direct correlation has been observed between recruitment of glass eels of *A. rostrata* and later production (Casselman *et al.* 1997), suggesting that reduced glass eel recruitment is likely to carry through into the fishery. A similar relationship can be anticipated for *A. dieffenbachia*, although the large variability in growth rates (Jellyman 1997) and longevity will result in an indirect relationship and also a considerable lag between glass eel recruitment and entry of sub-adult eels into the commercial fishery.

The modelling approach we have used is quite simple and focuses on the objective without incorporating unnecessary or unknown areas. If the basic rule about choosing model complexity is 'let the data tell you' (Hilborn and Mangel 1997), then models of eel population dynamics should, in general, be simple. Complex models can be difficult to parameterize and calibrate, since both eels and eel fishers can be highly variable between habitats at various spatial scales and important parameters such as density, catchability and sex ratio are difficult to estimate. Simple approaches often require fewer data for parameterization and calibration, less computing power to run and less knowledge to understand what the model is doing. They can also be more robust and have better predictive power (e.g. Ludwig and Walters 1985; Punt 1988). Optimal model size is usually much smaller than intuition dictates (Hilborn and Mangel 1997).

Conclusion

Fisheries for adult eels can severely reduce the number of migratory eels produced, particularly for long-lived species such as *A. dieffenbachii*. For this species, even relatively light fishing pressure may remove virtually all female migrants. In this case, a portion of the stock must be protected to maintain egg production. This would be best achieved through a system of no-take reserves, as it is not feasible to protect a portion of the fished stock. Management must ensure that sufficient productive areas remain unfished to maintain the supply of recruits to the population. Since there are no reliable estimates of what proportion of unfished egg production is required, conservative management based on the precautionary principle must be applied. Because the generation time for female *A. dieffenbachii* may often exceed 40 years, changes in the fishery are likely to occur at time-scales too long for humans to notice easily. Changes in management will also require long periods to produce their full benefits. Population modelling has the marked advantage of being able to work at such scales and provide a predictive dimension to the responses of eel populations to changes in management.

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