

The Optimal Recovery of a Semelparous Fish Population with Delayed Recruitment

GRAEME J. DOOLE

Department of Applied and International Economics,
Massey University, Private Bag 11 222, Palmerston North,
New Zealand

ROBERT R. ALEXANDER

Department of Applied and International Economics,
Massey University, Private Bag 11 222, Palmerston North,
New Zealand

E-mail: R.R.Alexander@massey.ac.nz

Abstract: Annual recruitment of the New Zealand longfin eel (*Anguilla dieffenbachii*) has decreased by around 75 percent since heavy levels of commercial fishing began in the early 1970s. Given the unsustainability of existing regulatory policy, a deterministic multiple-cohort bioeconomic model is developed and applied to this system to gain insight into the optimal age structure and harvest profile for this species. This model illustrates that the rapid recovery of this fishery would rely on the ability of managers to sufficiently limit the harvest of more valuable year classes to allow for the rebuilding of spawning biomass. The importance of decreasing the degree of exploitation within the fishable population and lessening the time that longfins are available to harvest through higher minimum weight restrictions is also highlighted. The need for conservative management is reinforced when uncertainty regarding the effect of exploitation on fecundity and barriers to the successful instigation of these policies are considered.

1. INTRODUCTION

Since the onset of heavy commercial harvest in the early 1970s, annual recruitment of the New Zealand longfin eel (*Anguilla dieffenbachii*) has declined by around 75 percent (Jellyman et al. 2000). Although other factors, such as habitat loss and a changing ocean environment, would also have contributed, this species is especially sensitive to overexploitation given its biology and the disjointed regulation of its harvest. These characteristics highlight the need for an economic analysis of the fishery that provides insight into the dynamics of the problem, which biological analyses have yet to incorporate (for example Jellyman et al. 2000; Hoyle and Jellyman 2002, *in press*).

The identification and development of suitable management strategies for this species is problematic given the complexity of its biology. Like all anguillids the longfin is catadromous; that is, it spends a significant portion of its life in freshwater before reproducing in the sea. This makes the identification of a stock-recruitment relationship difficult, while also introducing a delay between spawning and the recruitment of young. Longfin eels are also semelparous, dying soon after making a single reproductive contribution. This complicates the management of the fishery as longfins who succumb to either fishing or pre-spawning natural mortality have yet to contribute to spawning (McCleave 2001). These difficulties are exacerbated through the extensive period (up to 100 years in some environments) that female longfins require to reach sexual maturity. These factors mean that the cumulative impact of even low levels of annual exploitation can have extremely deleterious effects on longfin populations.

Additionally, the regulation of the longfin fishery has historically lacked coherency. Weight and gear restrictions have failed to sufficiently protect spawning biomass (Chisnall et al. 2002, *in press*), while limits on individual effort or harvest did not exist for many years. The sustainability of the South Island fishery, under quota control since October 2000, is also questionable since regional Total Allowable Catch (TAC) levels have primarily been calculated using historical harvest figures (New Zealand Ministry of Fisheries 2000) that have caused severe recruitment overfishing. The lack of conservativeness in TAC formation and the inadequacy of other regulatory approaches highlight the need to gain insight into the optimal recovery and sustainable

management of the New Zealand longfin eel fishery. This is particularly evident when the significant costs associated with closing certain fisheries (see Chisnall and Hicks 1993; Jellyman et al. 2000; Hoyle and Jellyman 2002, *in press*) are considered.

Existing age-structured models are not suited for investigation of this problem. Deriso (1980) developed a framework that allows the description of semelparous populations with delayed recruitment, but it does not allow for the study of *individual* cohorts, which is required in this case given that the price received for harvested longfins increases with individual size (Anderson 1989). Additionally, while analytical investigations involving the Beverton-Holt model (Beverton and Holt 1957) have been developed by many authors (for example Clark 1990; Schott 2001), their assumptions of constant recruitment and density-independent growth are not applicable here. The complex nature of the problem and a lack of information also prevent the use of analytical methods based on a sole sustainability constraint for the maintenance of a minimum level of spawning biomass (Yamauchi et al. 1997). The need to include a stock-recruitment relationship and a comparative lack of data for the longfin also render the sophisticated stochastic models developed for an Italian eel fishery by De Leo and Gatto (1995, 2001) unsuitable.

In this research a multiple-cohort bioeconomic model is developed that incorporates a delay-difference relationship to portray the significant period of time between escapement for spawning and the attainment of harvestable size. The developed model is based on the generalised framework of Conrad (1982); however, this work is extended to include density-dependent stock-recruitment and growth relationships, classification according to both gender and life stage, delayed biological recruitment, and the examination of approach paths.

A brief background to the developed framework is provided in Section 2, followed by a description of the notation and units used in Section 3. This is followed by a description of the bioeconomic model and the solution procedure in Section 4. The biological and economic data sources are presented in Section 5, followed by a discussion of the results in Section 6. Section 7 summarises the primary conclusions of this work.

2. BACKGROUND

The longfin stock of the lower Waikato River is used as a basis for this analysis, as this area is relatively well studied, large enough to validate the use of a stock-recruitment function, and is representative of the entire fishery in that its longfin population is in an exploited state (Chisnall et al. 2002, *in press*).

Due to a lack of information, especially in regard to individual variation, this stock is studied in an aggregate form; because in the following age-structured model, the members of each age class are all treated as “average” animals, with uniform size, growth, mortality, and patterns of sexual maturity. The model also rests on an assumption that vital parameters are more related to age than size. This follows from the description of animals in each age class by a mean weight and length using data obtained from Beentjes et al. (1997) and Chisnall et al. (2002, *in press*). Therefore, although animals are classified by age, the importance of size in the determination of important relationships is retained.

A diagram of the longfin life cycle within the stock described by the model is provided in Figure 1. This life cycle represents a number of simplifying assumptions. First, females are assumed to take six months to swim to oceanic spawning grounds from their freshwater habitat with all cohort members reaching maturity at the same age. Second, it is assumed that young take eighteen months from the time they hatch in the ocean until they arrive in their freshwater home range. Therefore, the lag between escapement and the resulting biological recruitment of offspring (elvers or year class 0 within the model) is two years. Third, using the growth relationships mentioned above, eels are assumed to reach the current minimum harvestable weight at 11 years of age. Although this may be manipulated to portray the effects of different weight restrictions, the division between *juvenile* and *adult* classes is always assumed to exist between eels of 0 and 10 years of age and eels of 11 years and above, as depicted in Figure 1. This division arises from dimorphism in dietary preference, as eels below 40 cm in length (juveniles) feed from the substrate of their resident waterway, predominantly eating insect larvae and molluscs, while larger longfins (adults) are predominantly piscivorous (Jellyman 1996, 1997). It follows that since competition for food and space has a strong effect on the growth rates of larger eels (Chisnall

and Hicks 1993; Jellyman 1997), their growth within this model is classified as density-dependent while that for juveniles is not.

Sexual dimorphism is also included to cater for differences in age at sexual maturity. Since the limiting factor for longfin recruitment is the availability of spawning females (Jellyman et al. 2000; Hoyle and Jellyman 2002, *in press*), the spawner-recruitment relationship within the following model concerns only mature specimens of this gender. Alternatively, the migration of males (which occurs at much younger ages) is represented through the exit of these animals in a way that is synonymous with natural mortality. All females are assumed to mature at the age at which length is closest to that corresponding to the mean size of migrant female longfins (1156 mm) (Todd 1980), which is 31 years in this habitat. Alternatively, the way in which the maturity of males is dealt with allows for migration at a wider range of ages (year classes 12 to 18). Finally, this analysis assumes equal sex ratios for recruiting eels (Francis and Jellyman 1999; Jellyman et al. 2000).

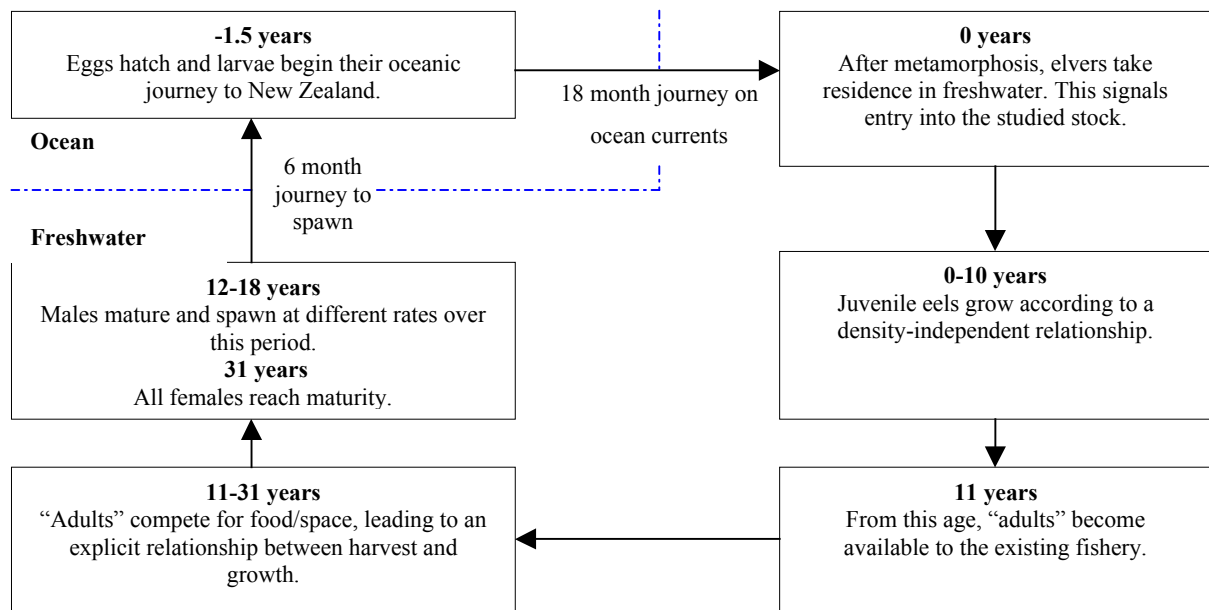


Figure 1: Generalised life cycle of the lower Waikato River eel stock.

3. NOTATION AND UNITS

The cohort references and subscripts used within this analysis are presented in Table 1. It is assumed that all animals between the ages of k^h and k^{s-1} have a constant rate of catchability and that perfect selectivity exists. This assumption provides for richer insight into the harvest profiles for individual cohorts given the nature of pricing (Anderson 1989) while also allowing for the comparison of alternative policies incorporating different weight restrictions. It is also assumed that all juvenile cohorts (those year classes below $k^a = 11$) are never harvested. This assumption follows the findings of Chisnall et al. (2002, *in press*) in that policies involving the manipulation of minimum weight restrictions should involve increasing existing limits.

Table 1: Description of cohort references and subscripts used within this analysis.

Subscript	Description	Value
t	Time in years	$t = [0, 1, \dots, \infty]$
ω	Delay between female escapement and the return of elvers	$\omega = 2$
k	Age in years	$k = [0, 1, 2, \dots, k^s]$, where $k = 0$ is the elver class and k^s is the eldest age group
k^m	The range of ages at which males reach sexual maturity	$k^m = [12, 13, \dots, 18]$

k^h	and migrate The youngest cohort vulnerable to gear, this can be altered to reflect different minimum weight restrictions	$k^h = 11$
k^H	The eldest harvestable cohort, this can also be altered to reflect different maximum weight restrictions	$k^H = 30$
k^a	The youngest adult cohort	$k^a = 11$
k^s	The spawning year class. This age group leaves the system without being harvested as migrating females are not exploited (Hoyle and Jellyman 2002, <i>in press</i>). Therefore $Y_{k^s,t} = 0$.	$k^s = 31$

The general variables used within this model are presented in Table 2. While the first two ($C_{k,t}$ and π) are measured in dollars, all stock and harvest variables are calculated in tonnes. In addition to the usual feasibility constraints presented in Table 2, it is assumed that the adult stock can never be larger than the virgin biomass ($X_0 = 690$ tonnes).

Table 2: Description of general variables used within this analysis.

Variable	Description	Unit/Restriction
$C_{k,t}$	Cost of harvesting cohort k at time t	Measured in dollars
π	Net revenue	Measured in dollars
$X_{k,t}$	The weight of eels in the k th cohort at time t	Measured in tonnes. In every period, $X_{k,t} \geq 0$
$Y_{k,t}$	The weight of eels harvested from the k th cohort at time t , for $k = [k^h, \dots, k^H]$	Measured in tonnes. In every period, $Y_{k,t} \geq 0$ and $X_{k,t} \geq Y_{k,t} \geq 0$
X_{AD}	The adult stock	$X_{AD} = \sum_{k=k^a}^{k^s} X_{k,t}$ In every period, $X_0 \geq X_{AD}$

The exogenous parameters used in this model are presented in Table 3. For an account of how each is estimated, see Section 5. It is assumed that stock dynamics and economic parameters remain the same over the period of study, despite the extended timeframe involved. While the latter is perhaps less appropriate than the former, this is necessary due to the lack of information regarding how they may change.

Table 3: Description of exogenous parameters used within this analysis.

Parameter	Description	Value/Unit/Source
c	Cost of harvesting one tonne of eels	$c = \$2071.26/\text{tonne}$
ρ	Discount factor	$\rho = 1/(1+r)$
r	Discount rate	$r = .05$
P_k	Price for harvested cohort k	$P_k = \$4350/\text{tonne}$ for $k = 11-14$, $P_k = \$4540/\text{tonne}$ for $k = 15-18$, $P_k = \$4850/\text{tonne}$ for $k = 19-20$, $P_k = \$5950/\text{tonne}$ for $k = 20-30$
a	Productivity parameter for spawner-recruitment function	$a = .014$
b	Density-dependence parameter for spawner-recruitment function	$b = .067$
G_k	Instantaneous annual rate of growth for juvenile cohort k	Identified from growth relationships in Chisnall et al. (2002, <i>in press</i>).
M	Instantaneous annual rate of natural mortality	$M = .04$

$\sum_{k=0}^{k^a} (G_k - M)$	Survival rate for juveniles	$\sum_{k=0}^{k^a} (G_k - M) = 4.65$
ϕ	Density-dependent growth factor	$\phi = .0004$
$\mu(k^m)$	Instantaneous rate of male migration as a function of age	$\mu(12) = -.015, \mu(13) = -.035, \mu(14) = -.105, \mu(15) = -.114, \mu(16) = -.177, \mu(17) = -.057, \mu(18) = -.025$

4. THE BIOECONOMIC MODEL

4.1 The Economic Model

Following the bioeconomic convention of specifying fisheries as capital stocks (Clark 1985), this analysis assumes the eel resource is owned by a sole manager who aims to maximise net present value. This approach allows the consideration of important economic factors that are missing in biological models of the longfin fishery.

The estimation of a standard production function (see Clark 1985) is problematic given the lack of corresponding annual harvest, stock, and effort data for this fishery. The validity of this approach is also questionable, given recent findings disputing the inclusion of exogenous population data in these specifications (Schott 2002). Following Conrad (1982), the inverse relationship between costs and stock levels is therefore alternatively represented through the inclusion of a harvest-stock ratio term in the cost function:

$$C_{k,t} = c \cdot Y_{k,t} \cdot \left(\frac{Y_{k,t}}{X_{k,t}} \right) \quad (1)$$

Since there is no apparent terminal period for the fishery, this problem is cast as an infinite-horizon problem. It therefore follows that the level of total discounted net revenues (π) accruing to the harvest of the studied eel stock can be expressed as:

$$\pi = \sum_{t=0}^{\infty} \rho^{t-1} \left(\sum_{k=k^h}^{k^H} Y_{k,t} \cdot \left(P_k - c \cdot \left(\frac{Y_{k,t}}{X_{k,t}} \right) \right) \right) \quad (2)$$

Although price increases with size in reality, in this model it is represented through a price that increases with age.

4.2 The Biological Model

The net revenue function presented in equation (2) is maximised according to constraints representing changes in the eel stock over time occurring through both natural effects (growth, migration, recruitment, and natural mortality) and harvest. Following the life cycle depicted in Figure 1, these processes are represented in the following ways.

In a given year t , the elver stock will depend on the spawning stock of ω years before. A Beverton-Holt spawner-recruitment relationship (Beverton and Holt 1957) is assumed, as it is hypothesised that young on their oceanic journey are vulnerable to predation and compete for food due to a limited swimming ability. Due to the lag between escapement and the return of elvers into the system (ω), this is expressed in the following delay-difference equation:

$$X_{0,t+\omega} = \frac{a \cdot X_{k^s,t}}{1 + b \cdot X_{k^s,t}} \quad (3)$$

From this the “recruitment” constraint is formulated. This constraint describes the size of the first adult cohort (k^a) as a function of the spawning biomass $\omega + k^a$ years before. As juveniles are not harvested and are subject to density-independent survival, this equation is:

$$X_{k^a,t+\omega+k^a} = \frac{a \cdot X_{k^s,t}}{1 + b \cdot X_{k^s,t}} \cdot e^{\sum_{k=0}^{k^a} (G_k - M)} \quad (4)$$

Additionally, the “growth” constraint describes the way in which the weight of any *adult* cohort changes over time through physical growth, natural mortality, the migration of males at maturity, and harvest. This can be seen in the following expression:

$$X_{k+1,t+\omega+k^a+1} = X_{k,t+\omega+k^a} \cdot e^{\phi(X_0 - X_{AD}) - M - \mu(k^m)} - Y_{k,t+\omega+k^a} \quad (5)$$

The specification of this equation contains a number of important factors. First it demonstrates that growth, natural mortality, and the migration of males occurs before harvest in each period. Second, a density-dependent growth term for adults ($\phi(X_0 - X_{AD})$) is included. As in the popular logistic function, this specification shows that at virgin biomass (assumed to be the carrying capacity of the environment) there will be no growth. However, as the current stock level falls, growth will increase as eels compete less for food and space.

Alongside the feasibility constraints; $X_{k,t} \geq 0$, $Y_{k,t} \geq 0$, and $X_{k,t} \geq Y_{k,t} \geq 0$, equations (2), (4), and (5) specify a discrete-time optimal control model (Clark 1985, 1990), where $X_{k,t}$ and $Y_{k,t}$ denote the state and control variables respectively. This framework could easily cater for the addition of stochasticity; for example multiplying the stock-recruitment function by a white noise variable may provide for more realism given that longfin recruitment is highly variable. A deterministic approach is retained as such an addition is likely to have only a minimal effect on the results (Clark 1985).

4.3 Solution Procedure

The model is solved using Nonlinear Programming (NLP) through the utilization of the CONOPT2 solver in the General Algebraic Modelling System (GAMS) (Brooke et al. 1988). To solve this infinite-horizon problem using GAMS software it is truncated to a finite horizon of significant length (75 years). Terminal periods with divergences from the steady-state optimum are disregarded as artefacts from truncation, as experiments with the model over longer periods showed the initial equilibrium to indeed be optimal.

5. MODEL DATA FOR THE LONGFIN EEL

5.1 Economic Data

The initial discount rate (r) is 5 percent, the mean annual real 10-year secondary market government bond rate for December 1994 to December 2001. The prices (P_k) used in this analysis are drawn from telephone interviews with New Zealand’s five major eel processors. The harvesting cost parameter (c) is drawn from a survey of harvesters who are licensed to fish in the study region. This parameter includes the opportunity cost of employment.

5.2 Biological Data

The area of the study region is identified using Geographic Information Systems (GIS). An estimate of the virgin stock level is then obtained using this and density data from Chisnall et al. (2002, *in press*). Following Campbell et al. (1993), a simulation model is developed using this estimate of the virgin stock and is used to generate equilibrium values of the adult stock (X_{AD}) and corresponding growth rates ($g(X_{AD})$) for a wide range of fishing mortality values. ($X_0 - X_{AD}$) and $g(X_{AD})$ are then regressed to identify a value for the density-dependent growth factor (ϕ). Initial cohort sizes are identified using this model and an exploitation rate of 20 percent, which Jellyman et al. (2000) highlighted as adequately describing historical harvest rates in one waterway. Instantaneous growth rates for each discrete growth period between birth and entry into the first adult cohort (k^a) are identified using growth relationships from Chisnall et al. (2002, *in press*). The rate of natural mortality (for both juveniles and adults) is taken from Francis and Jellyman (1999). The instantaneous rate of male migration for each affected age class ($\mu(k^m)$) is calculated from data in Todd (1980) and Chisnall et al. (2002, *in press*). The estimation of a stock-recruitment relationship for the longfin is difficult given the high variability of recruitment and the lack of available information. However following Ricker (1975), a theoretical approach to estimating a Beverton-Holt relationship is developed and applied to the studied stock.

6. RESULTS AND DISCUSSION

The model is formulated to mimic the current management of the North Island longfin fishery in that only a minimum weight restriction (220 g) (consistent with $k^a = k^h$) is represented. This formulation provides some insight into the nature of optimal harvest profiles arising from the model described in Section 4.

The optimal stock levels for the first 40 years are displayed in Figure 2. It can be seen that the long-run equilibrium stock level is much lower than the virgin biomass ($X_0 = 690$ tonnes). This highlights that as long as spawning biomass is sufficient to sustain the population, it is optimal to have a significantly lower stock level so that the sole owner may benefit from increased growth due to the lessening of competition among adults. Even though the longfin is slow-growing and experiences delayed recruitment, the latter of which significantly prolongs the length of time required before a long-run equilibrium is reached, this low level of steady-state biomass (and subsequent rapid growth rate) decreases the time required for the stock to recover from its exploited position. However the length of this recovery period is heavily reliant on exercising the optimal harvest profile identified by the model.

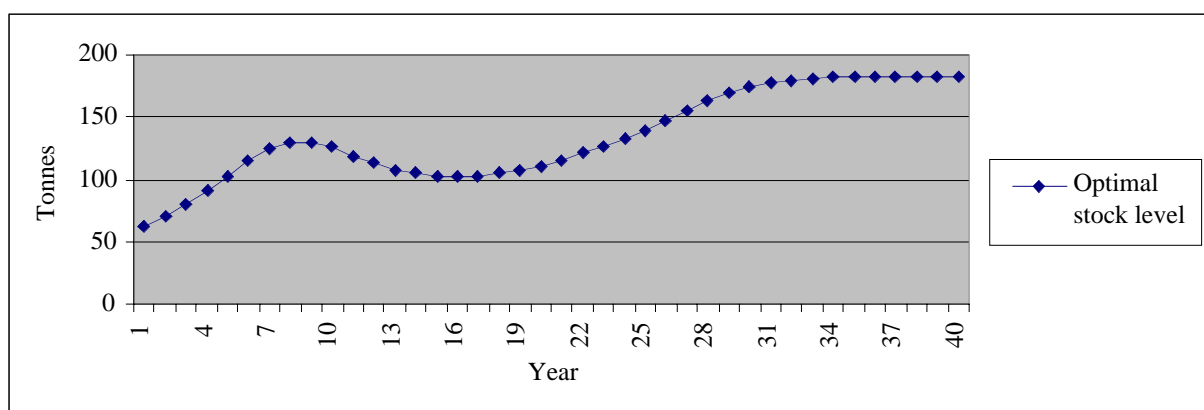


Figure 2: Optimal stock levels.

Cohorts are only lightly cropped during the first four years of recovery, however from year five the harvest of more valuable age classes (year classes 21 to 30, which are all female) (see Table 3 for relative monetary values) increases steadily until the equilibrium age structure portrayed in Figure 3 is obtained. The intuitive

concentration of harvest on the most valuable cohorts within a population has been demonstrated previously (Conrad 1982; Moyle 1999), however in regard to the longfin fishery this finding has a number of important implications. First, this highlights the inefficiency of the recommendation for lower maximum weights presented by various authors (Chisnall and Hicks 1993; Chisnall et al. 2002, *in press*; Hoyle and Jellyman 2002, *in press*). For example the protection of all eels above 1.5 kg (Chisnall and Hicks 1993) would prevent the harvest of all eels within the most valuable year classes within this model. Although this may be biologically favourable, removing these year classes from the fishery will involve significant inefficiency given that it involves a significant divergence from the optimal age structure. Second, the minimal harvest of less valuable year classes (220 g to 1.4 kg, or ages 11 to 20 within this model) displays that significant benefits in regard to overcoming growth overfishing can be made through increasing the minimum weight restriction to 1.5 kg. This displays the inefficiency of current exploitation, as the majority of harvested eels are now less than 500 g in weight (Beentjes 1999). However though this would sufficiently protect all males from exploitation as all spawn beneath this weight (Todd 1980), this highlights the importance of limiting the harvest of females to moderate levels as such a weight restriction merely delays the harvest of this longer-living gender.

The optimal age-structure outlined in Figure 3 involves the removal of the large majority of the penultimate year class and leaving only a small fraction to breed (18.7 percent). This displays the high economic

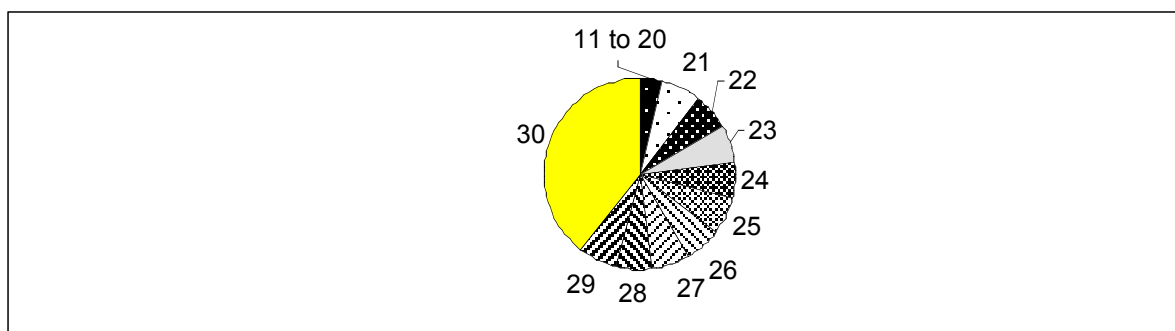


Figure 3: Composition of the equilibrium harvest level according to fishable year classes 11 to 30.

value of the pre-spawning year class, as this cohort has obtained maximum benefits from high annual growth rates arising from a low adult stock level. Since fishing pressure can be controlled perfectly in the model, it follows that the sole owner maximises harvest from this cohort and leaves the absolute minimum spawning biomass required to maintain the equilibrium population. This result has much to do with the relatively high economic value of these animals and the diminishing returns to increasing spawning biomass arising from the concavity of the Beverton-Holt spawner-recruitment function used within this framework.

The optimal harvest levels for the first 40 years are displayed in Figure 4. The optimal recovery policy requires that harvest is maintained at low levels for the first 5 years, highlighting that strategic use of moratoriums would play a key role in the rapid recovery of these stocks. Low initial harvest levels mean that spawning biomass can increase to its steady-state value (3 tonnes) rather rapidly (6 years). Low stock levels mean that although exploitation is minimal during this time, the stock is growing quickly and thus only a short period of recovery is required until a higher level of fishing may be sustained. However this lower level may also render stocks less able to resist environmental disturbances, and thus increases the susceptibility of these populations to overharvest.

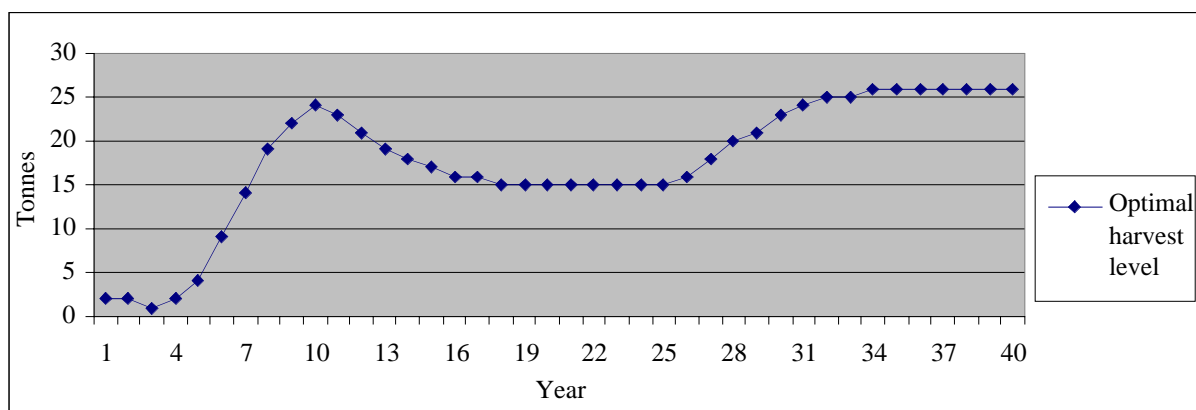


Figure 4: Optimal harvest levels.

The equilibrium exploitation rate in regard to the optimal stock level is moderate (14.2 percent), being significantly lower than an estimate of 20 percent used to describe historic harvest levels by Jellyman et al. (2000). This illustrates the large effect that even sensible rates of annual exploitation have on eel populations due to their extreme biology as the corresponding level of stock in equilibrium (183 tonnes) (Figure 2) is well below the virgin biomass ($X_0 = 690$ tonnes). In reality, difficulties associated with instigating the optimal age-structure (Figure 3) and harvest profile (Figure 4) will exist due to industry pressure against decreased harvests, imperfect selectivity, uncertainty surrounding stock levels, and the economic incentive for harvesters to remove even those animals required to sustain recruitment. This highlights the necessity for conservativeness and therefore the insufficiency of current quota-setting methodology involving the persistence of historical harvest rates.

However there remains some concern surrounding the optimal exploitation rate identified above, as this model assumes that fecundity remains unaffected when populations diminish to lower levels. This is clearly an important simplification as egg production commonly falls as the rate of fishing builds (Jennings et al. 2001). This highlights the importance of identifying the effect that harvest has on the fecundity of longfins, as this presents the possibility of extinction given their sensitivity to exploitation arising from their complex biology and current rates of exploitation.

7. CONCLUSIONS

The rapid recovery of this fishery relies on the use of a moratorium and the ability of managers to sufficiently limit the harvest of more valuable year classes to allow for the rebuilding of spawning biomass. Slow growth and delayed recruitment lengthen the time required before a steady-state is reached, however the low level of biomass during recovery and subsequent rapid growth arising from less competition promote rebuilding towards

a stock level where constant exploitation may be maintained. Through the maintenance of this constant level of harvest after recovery, the costs of closure can be avoided and a smaller, more viable industry can be maintained. Additionally the costs of reducing industry size will be lower than in many ocean fisheries, given the low capital value of gear.

Furthermore, this model illustrates the importance of introducing a significantly higher minimum weight restriction to help overcome growth overfishing. However the failure of the optimal level identified by the model (1.5 kg) to sufficiently protect longer-living females highlights the significance of limiting their harvest to moderate levels so that spawning biomass is sufficient to maintain populations. By decreasing the time that animals are available for harvest and decreasing the degree of exploitation within the fishable population, the greatest economic gain may be made from this difficult situation whereby more valuable cohorts and those approaching spawning are not separate, as in the analyses of Conrad (1982) and Moyle (1999). However this strategy presents significant practical difficulties for managing this fishery to optimise efficiency, given poor stock information and the economic incentive for harvesters to target larger females before they spawn.

This model also demonstrates the insufficiency of using historical harvest data to estimate suitable quota levels, given the biology of the longfin and uncertainty regarding the effect of exploitation on fecundity. The complexity of the problem, environmental variation, and the lack of information surrounding key features of the system compound the necessity for conservativeness, given that these increase the difficulty of formulating suitable models and effective management policies. These findings and the current state of the longfin fishery highlight the urgency with which conservative quotas and appropriate weight restrictions should be introduced. The future identification of these are important goals for which this model is well suited.

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