

The University of Maine
DigitalCommons@UMaine

Marine Sciences Faculty Scholarship

School of Marine Sciences

5-1-2004

Male Dominance in the New Zealand Longfin Eel Population of a New Zealand River: Probable Causes and Implications for Management

James McCleave

University of Maine - Main, mccleave@maine.edu

D.J. Jellyman

Follow this and additional works at: https://digitalcommons.library.umaine.edu/sms_facpub

Repository Citation

McCleave, James and Jellyman, D. J., "Male Dominance in the New Zealand Longfin Eel Population of a New Zealand River: Probable Causes and Implications for Management" (2004). *Marine Sciences Faculty Scholarship*. 69.
https://digitalcommons.library.umaine.edu/sms_facpub/69

This Article is brought to you for free and open access by DigitalCommons@UMaine. It has been accepted for inclusion in Marine Sciences Faculty Scholarship by an authorized administrator of DigitalCommons@UMaine. For more information, please contact um.library.technical.services@maine.edu.

Male Dominance in the New Zealand Longfin Eel Population of a New Zealand River: Probable Causes and Implications for Management

JAMES D. MCCLEAVE*

School of Marine Sciences, University of Maine,
Orono, Maine 04469-5741, USA

DONALD J. JELLYMAN

National Institute of Water and Atmospheric Research, Ltd.,
Post Office Box 8602, Christchurch, New Zealand

Abstract.—The endemic New Zealand longfin eel *Anguilla dieffenbachi* (hereafter, longfin eel), is overfished, and in southern South Island, New Zealand, rivers have recently become predominated by males. This study examined length and age at sexual differentiation in male eels in the Aparima River catchment (area, 1,375 km²; mean flow, 20 m³ · s⁻¹) and the sex ratio and distribution of eels throughout the catchment. Longfin eels differentiated into males mostly at lengths from 300 to 460 mm and ages from 10 to 25+ years. Females were rare: Of 738 eels examined for sexual differentiation, 466 were males and 5 were females, and a few others, not examined, were large enough to be female. These counts suggest a male : female ratio among differentiated longfin eels of 68:1. Of 31 differentiated shortfin eels *A. australis*, less common in the Aparima River, 26 were females. Male longfin eels were distributed throughout the main stem and tributaries; undifferentiated eels were more prevalent in lower and middle reaches and in the main stem than in upper reaches and tributaries. In other studies, male longfin eels predominated commercial catches in the Aparima and four other southernmost rivers, by 2.4:1 to 13.6:1 males to females. The Aparima River had the most skewed sex ratio. Longfin eel catches from the Aparima River will become more male predominated because few sublegal-size females were present. The length-frequency distributions of eels in the present samples and in the commercial catches were truncated just above minimum legal size (about 460 mm), showing that few females escape the fishery. Historically, females predominated these rivers. The recent change in sex ratio is attributable partly to selective harvest of females, and partly to changes in the structure of the population from fishing, such that differentiation into males has been favored. Longevity, delayed sexual maturity, semelparity, and endemism with restricted range make the longfin eel particularly vulnerable to overfishing.

The two principal species of catadromous eels in New Zealand, the New Zealand longfin eel *Anguilla dieffenbachi* (hereafter, longfin eel) and the shortfin eel *A. australis*, are native and widespread in freshwaters of both the North and South islands (McDowall 1993, 1998). The endemic longfin eel penetrates farther inland and to higher elevations (McDowall 1993, 1998), inhabiting river systems from estuaries (Jellyman et al. 1997) to high country lakes (Jellyman 1995). The inland penetration of the longfin eel, especially, has been restricted in some catchments (i.e., drainages) by the construction of hydroelectric dams (Jellyman 1995; Boubée et al. 2001).

Commercial fishing of yellow-phase (i.e., resident) eels of both species has been intensive in

most catchments. The mean annual commercial catch of eels in New Zealand for 9 years in the 1990s was estimated at 1,140 metric tons (Beentjes and Bull 2002). Longfin eels constituted about 30% of the commercially landed weight of eels in New Zealand, but they composed about 80% of landed weight in river catchments of the South Island, excluding one large lowland lake (estimated from data in Beentjes 1999; Chisnall and Kemp 2000; Beentjes and Bull 2002). Being ubiquitous and plentiful, freshwater eels were of enormous importance to early Maori (New Zealand's indigenous people; McDowall 1990), who continue to harvest eels for traditional purposes.

Concern over the well-being of the longfin eel stock has been expressed for some time (Chisnall and Hicks 1993; Jellyman 1995; Hoyle and Jellyman 2002). Evidence supporting that concern, especially for the South Island, comes from (1) studies monitoring commercial harvesting (Be-

* Corresponding author: mcclleave@maine.edu

Received March 4, 2003; accepted July 16, 2003

entjes and Chisnall 1997, 1998; Beentjes 1999; Chisnall and Kemp 2000), (2) a decline in mean weight of individual longfin eels in commercial catches from the 1970s to 1990s (Beentjes and Chisnall 1997), (3) a decline in catch per unit effort through the 1990s (Beentjes and Bull 2002), (4) sex ratios skewed toward male predominance in recent commercial catches from several catchments (Beentjes and Chisnall 1998; Beentjes 1999), and (5) apparent declining recruitment of juvenile longfin eels (Glova et al. 2001). Recent modeling incorporating realistic values for exploitation rates led to the conclusion that longfin eels are severely overfished with respect to recruitment (Hoyle and Jellyman 2002).

Sex ratios of *Anguilla* species vary widely among locales, both naturally and as a result of manipulation. For example, silver-phase (i.e., seaward migrating) American eels *A. rostrata* in five lightly exploited or unexploited rivers in the northeastern USA ranged from 49% to 98% male (Oliveira et al. 2001). About 250 km away but at the same latitude in Canada, two rivers exploited for migrating silver eels had 0% and 3% males (Jessop 1987). The sex ratio of silver European eels *A. anguilla* migrating from an Irish lake changed gradually from 9% male to 86% male within a decade, attributable directly or indirectly to elver stocking (Parsons et al. 1977; Kennedy and Vickers 1990). The sex ratio of silver shortfin eels in Lake Ellesmere, New Zealand, changed from female predominance (78%) in the 1940s to male predominance (>99%) in the 1990s, which has been attributed to effects of commercial fishing and ecological changes in the lake (Jellyman and Todd 1998).

Four features of the unusual life cycle of anguillids generally, and longfin eels specifically, make eels an intriguing group for study and an enigma for traditional fisheries management. First, sexual differentiation is environmentally determined (Colombo and Rossi 1978; De Leo and Gatto 1996; Holmgren 1996; Krueger and Oliveira 1999), high population density being strongly implicated in increasing the proportion of males and vice versa (e.g., Colombo and Rossi 1978; Egusa 1979; Naismith and Knights 1990; Holmgren 1996; Roncarati et al. 1997; Krueger and Oliveira 1999). This means that typical management practices may have unanticipated consequences. Second, anguillids are panmictic species (Avisé et al. 1986; Sang et al. 1994; Lintas et al. 1998; Bastrop et al. 2000) or nearly so (Chan et al. 1997; Wirth and Bernatchez 2001), including the New Zealand

species (Smith et al. 2001). This means that heavily fished areas can obtain recruitment from the progeny of eels from other areas, so long as eels exist in the other areas. Third, because anguillids are semelparous, they may contribute to spawning or to human harvest, but not both. Fourth, anguillid eels, and especially female longfin eels, grow slowly and reach sexual maturity only after decades. Longfin eels may reach legal commercial size (220 g) after 10–20 years (Chisnall and Hicks 1993; Beentjes and Chisnall 1998). However, ages of migrating silver eel females ranged from 25 to 60 years in lowland areas (Todd 1980) to an estimated mean of 93 years in a high country lake (Jellyman 1995). This means that females may be vulnerable to the commercial fishery for several decades.

An endemic, late-maturing species with a restricted geographic range, such as the longfin eel in New Zealand, may be particularly susceptible to overfishing and the threat of extinction (Parent and Schriml 1995; Sadovy 2001). Further, high fecundity, also characteristic of the longfin eel, does not reduce the risk of overfishing, as is often mistakenly assumed (Sadovy 2001).

The need for information on sexual differentiation and sex ratio for modeling of population dynamics, coupled with the evidence for skewed sex ratios in some southern rivers, prompted us to examine sex distribution as part of a wider program investigating recruitment and survival of longfin eels in the exploited Aparima River catchment. Samples of commercial catches in the Aparima River during the fishing seasons of 1996–1997 and 1997–1998 indicated that 93% of longfin eels with macroscopically identifiable gonads were males (Beentjes and Chisnall 1998; Beentjes 1999).

The objectives of this study were to examine longfin eels in the Aparima River catchment to determine (1) the length and age of sexual differentiation, and (2) the sex ratio and distribution of the sexes within the catchment. Although this paper focuses on longfin eels, information on the rarer shortfin eels in the catchment is included for comparison. Because female longfin eels were found to be rare, much of the analysis was necessarily restricted to sexually undifferentiated and male eels. We also considered whether male predominance is a natural phenomenon, a function of selective harvest of females, or a product of change in factors causing sex determination.

Study Area

The Aparima River catchment of 1,375 km² (Robertson 1992) is at the south end (Southland

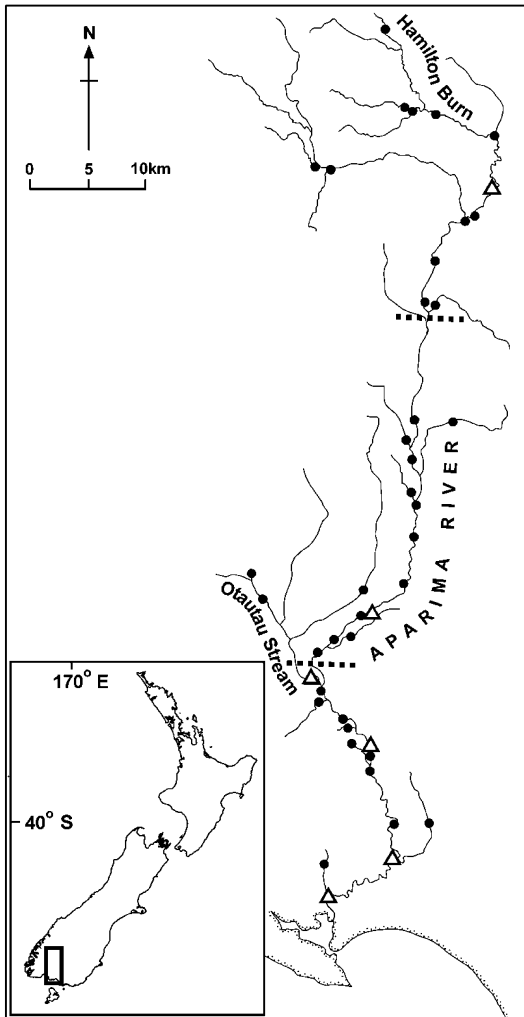


FIGURE 1.—Map of the Aparima River catchment, New Zealand, showing electric fishing (solid circles) and fyke netting (open triangles) sites for longfin eels. Horizontal dotted lines separate the catchment into lower, middle, and upper reaches. Numerous small tributaries not shown. The inset locates Aparima catchment on the South Island of New Zealand.

Region) of the South Island, New Zealand, and flows into the South Pacific Ocean at $46^{\circ}20.5'S$ and $168^{\circ}0.5'E$ (Figure 1). The Aparima River main stem, is 113 km long and has two main tributaries, the Otautau Stream and Hamilton Burn, and numerous smaller tributaries and constructed drains of adjacent lands. It is mostly a single-thread river, although the section between Otautau Stream and Hamilton Burn is somewhat braided. The main stem, especially the upper half, is steep and swift-flowing, but swampy, slow-flowing areas occur in

the Hamilton Burn catchment and in tributaries and constructed drains in the lower Aparima catchment (Robertson 1992). The catchment contains no lakes, and the river system is not dammed. Mean flow is approximately $20 \text{ m}^3 \cdot \text{s}^{-1}$ (Duncan 1992), but large departures from the mean occur.

The headwaters of the Aparima River and a few of the tributaries arise in forested mountains well above 1,000 m. However, 55% or more of the catchment is farmland devoted to growing crops, dairying, and raising sheep, cattle, and deer (Robertson 1992). The substrate varies through the catchment. Most of substrate in the main stem consists of fine and coarse gravel and cobbles and some boulders and exposed bedrock; there is little aquatic vegetation. Substrate in the various tributaries includes fine material, sand and mud, and gravels and cobbles; most have aquatic algae and macrophytes. Overhanging bank vegetation along the main stem and tributaries is absent to dense (willows *Salix* spp. and scrub trees). Yellow-phase longfin and shortfin eels are fished commercially with fyke nets in the main stem and the major tributaries.

This study was conducted from the upper estuary of the Aparima River to 117 km inland and included the main stem and its tributaries. Relevant findings from other southern rivers were also examined, principally from the nearby Waiu River (about 30 km to the west) and the Oreti and Maitai rivers (about 15 and 55 km east) in the Southland Region and the Clutha and Taieri Rivers (about 130 and 150 km east) in the adjacent Otago Region.

Methods

Field sampling.—Eels were collected in February 2001 at 45 sites by electric fishing and in February 2002 at 15 sites by electric fishing and at six sites with baited fyke nets (Figure 1). Electric fishing was done by wading primarily in riffles and runs, and to a lesser extent in willow-shaded pools and debris clusters, of the main stem and larger tributaries and in all habitats present in the smaller tributaries.

Fyke netting was done in the main stem and two largest tributaries where pools and deep runs were too deep to electric fish. We fished 8 or 10 nets in a linear series, approximately 30 m apart, overnight for 2 or 3 nights at each site; in addition, 3 nets were set over 1 night at a tidal site near the upper limit of salt penetration in the estuary. Mesh was 25 mm stretch measure.

At streamside, eels were anesthetized in a so-

lution of 2-phenoxyethanol, identified to species, and measured to the nearest millimeter total length. In 2001, samples of longfin eels, nearly all less than 400 mm long, were killed by overdose of anesthetic and frozen for later determination of age and sex. In 2002, samples of longfin eels, mostly 300–600 mm long, were similarly frozen for later determination of sex. Samples of longfin eels were chosen to represent all reaches of the catchment and from both main-stem sites and tributaries (Table 1). In 2001, samples emphasized sublegal-size eels, whereas in 2002, the samples covered the entire size range for which it was reasonable to expect some sexual differentiation. Also in 2002, a small sample of shortfin eels was kept for sex determination. All eels not kept were allowed to recover and were returned to the streams.

Sex determination.—The gonads of yellow eels lie as long ribbons from approximately the level of the liver to beyond the vent on each side of the body cavity along the junction of the swim bladder and body wall. Sex of longfin and shortfin eels was determined using criteria given by Todd (1974): undifferentiated gonads (stages 1, 2) = thin ribbons of uniform density that lack distinct lobes; early developing testes (stages 3, 4) = distinct white opaque zones joined by clear areas of tissue, the opaque zones becoming lobed; early developing ovaries (stages 6, 7) = an opaque ribbon with an anastomosing network of veinlike structures, which subsequently become a frilled ribbon with closely spaced transverse ridges on the lateral face.

To determine sex, each eel was thawed, the abdomen cut open from vent to pectoral girdle, and the left body wall was cut and laid open to expose the gonad. Intact gonads first were examined under a binocular microscope at 8–20 \times magnification. Sometimes, a drop of blue Wright's stain was placed along the intact gonad, and it flowed under the gonad by capillary action. In many cases, a small piece of gonadal tissue was removed (before any stain was added) and placed on a microscope slide with a few drops of aceto-carmin stain, which selectively stains gonad tissue (Guerrero and Shelton 1974). After a few minutes, the tissue was squashed with a cover slip or just covered with a cover slip, and examined with a compound microscope at 40–200 \times magnification.

Eels were classified as undifferentiated if the intact gonad was a transparent or translucent ribbon lacking opaque whitish areas, and if the gonad tissue resisted being squashed and showed uniform absorption of the aceto-carmin stain. Eels were

classified as males if there were developing, regularly spaced, whitish opaque areas separated by transparent tissue, even if the opaque areas did not extend the full length of the gonad. The presence of even early developing lobes was highlighted by the addition of blue stain to the body cavity. Also, developing testicular tissue resisted squashing and the developing lobes absorbed aceto-carmin, whereas the tissue between lobes scarcely did so. Eels were classified as females if the intact gonad was a frilly ridged ribbon. Such gonads had a soft texture, squashed easily, and clearly showed developing oocytes under the compound microscope. In one case, a smaller female was identified on the basis of an anastomosing veinlike network.

Age determination.—In 2001, ages were determined for 362 longfin eels (>100 mm) from throughout the catchment (Table 1). All but five eels were less than 400 mm long, and all were less than 437 mm. Aging was by the sawing and burning method described by Graynoth (1999). Briefly, saggital otoliths were removed from each eel, placed concave or convex side up on a strip of double-sided adhesive tape, and held in place with a strip of transparent tape. One otolith was sawn along the transverse plane through the nucleus with a fine scalpel under a binocular microscope. The two halves were placed on a scalpel blade and heated for 10–15 s over a high temperature gas flame. The halves were then mounted, cut side down, in clear silicone sealant on glass slides (Hu and Todd 1981). After the silicone cured, slides were inverted and examined under reflected light with a compound microscope at 50–400 \times magnification. Annuli were counted along the long ventral axis. Age is reported as the number of years in freshwater.

Data analysis.—Only eels 100 mm or longer were included in our analyses because shorter eels are not sampled adequately by electric fishing (105 longfin eels and 7 shortfin eels were excluded). Although we aged 228 longfin eels, we examined the testes of only 40 in the size range 240–280 mm and found 39 were undifferentiated. We assumed that the unexamined testes of the remaining 188 aged-only eels were also undifferentiated.

To analyze eel distribution by sex within the catchment, data from 2001 and 2002 were combined. Many more eels were measured than were both measured and sexed (Table 1). However, all those measured but not sexed that were less than 280 mm long were assumed to be undifferentiated. Further, of those measured but not sexed, all longfin eels 680 mm or longer and all shortfin eels 540

TABLE 1.—Numbers and size ranges (mm, in parentheses) of New Zealand longfin eels and shortfin eels 100 mm or longer measured, sexed, and aged in the Aparima River catchment, New Zealand, in February 2001 and 2002. One estuarine site is included in the categories lower reach and main stem.

Species	Sites and eel category	Catchment reach		
		Lower	Middle	Upper
Collection year 2001				
Longfin eel	Electric fishing sites	11	17	17
	Eels measured	436 (100–882)	424 (102–1,008)	232 (140–1,000)
	Eels sexed and aged	79 (226–437)	45 (244–395)	50 (268–398)
	Eels aged, not sexed	102 (100–276)	47 (108–272)	39 (157–276)
	Eels sexed, not aged	1 (353)	1 (495)	1 (348)
Shortfin eel	Eels measured	25 (161–926)	10 (125–531)	7 (120–792)
Collection year 2002				
Longfin eel	Electric fishing sites	4	8	3
	Fyke netting sites	4	1	1
	Eels measured	1,117 (100–746)	733 (104–729)	263 (213–670)
Shortfin eel	Eels sexed	200 (246–746)	251 (123–602)	110 (253–670)
	Eels measured	35 (106–812)	39 (112–733)	4 (398–605)
	Eels sexed	20 (355–605)	23 (276–667)	4 (398–605)

mm or longer were assumed to be females. Males can exceed these lengths, but based on sampling of the commercial landings from the Aparima catchment (Beentjes and Chisnall 1998; Beentjes 1999), our assumption would result in less than 5% misclassification. For some considerations, we apportioned longfin eels between 280 and 680 mm that were measured and released (i.e., not sexed) to undifferentiated male or female categories on the basis of percentages of males and females present in each size-class of those that were kept and examined for sex.

The minimum legal weight for commercially harvested longfin and shortfin eels in the South Island is 220 g. Using length–weight relations of Beentjes and Chisnall (1997, 1998), Beentjes (1999), and Hoyle and Jellyman (2002), 220 g corresponds to lengths of about 450 mm and 470 mm for longfin and shortfin eels, respectively.

Results

Longfin Eel Length and Age at Sexual Differentiation

Longfin eels differentiated into males over a narrow range of lengths in the Aparima catchment. About 50% of eels examined were differentiated by a length of 350 mm and 95% were differentiated at 450 mm (Figure 2). This statement must be qualified because recognition of gonadal differentiation was made without examination of histologic sections.

Longfin eels differentiated into males over a wide range of ages. Eels 100–437 mm long ranged in age from 1 to 30 years (Figure 3). Males were

present as a small proportion, beginning at age 10, but a high proportion was still undifferentiated around age 20. At ages 17–22, we found 70% of those aged were still undifferentiated. However, the proportion undifferentiated at the greater ages is biased somewhat high because the eels that differentiated at younger ages were the faster growing ones (Figure 4). In each age-class exceeding 9 years, the longest eels are the ones that are differentiated. Many of the faster growing males in the population were larger than the lengths we sampled for aging (mostly <400 mm). Only one female longfin eel, 368 mm long and 20 years old, was in the sample of eels we aged.

Shortfin Eel Length at Sexual Differentiation

Too few shortfin eels were examined for sex to allow conclusive statements about size at differentiation in the Aparima catchment. Of the 47 examined, 16 were undifferentiated (276 to 454 mm), 5 were males (378 to 530 mm), and 26 were females (397 to 667 mm).

Longfin Eel Sex Ratio and Distribution

Female longfin eels were rare in the Aparima catchment. Of 738 longfin eels examined for sexual differentiation, 466 were male and only 5 were female, and all five were in the lower reaches of the catchment. The four largest females were caught in a stretch of one small tributary; the fifth (smallest) was caught in the main stem. Based on length and sex data, about 26 of the largest longfin eels captured were probably females, including the four just mentioned and others not sexed. If the

TABLE 1.—Extended.

Species	Stream category		
	Main stem	Tributary	Total
Collection year 2001			
Longfin eel	15	30	45
	575 (100–830)	517 (140–1,008)	1,092 (100–1,008)
	96 (226–419)	78 (244–437)	174 (226–437)
	137 (100–276)	51 (157–276)	188 (100–276)
Shortfin eel	1 (353)	2 (348–495)	3 (348–495)
	7 (161–926)	35 (120–792)	42 (120–926)
Collection year 2002			
Longfin eel	7	8	15
	4	2	6
	1,565 (100–729)	548 (122–746)	2,113 (100–746)
Shortfin eel	385 (123–670)	176 (253–746)	561 (123–746)
	32 (106–812)	46 (174–733)	78 (106–812)
	21 (355–605)	26 (276–667)	47 (276–667)

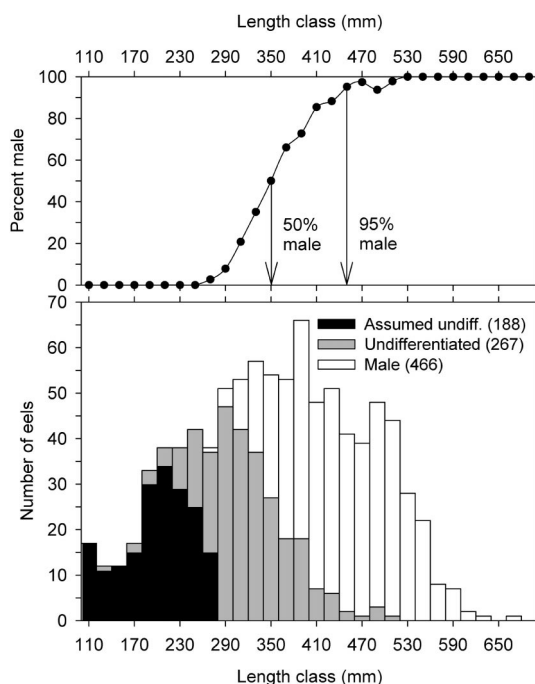


FIGURE 2.—Length-frequencies of New Zealand longfin eels from the Aparima River catchment, classified as undifferentiated or male (lower panel) and the percentage differentiated into males at each length class (upper panel). Arrows mark lengths at which 50% and 95% of the eels were differentiated into males. The assumed undifferentiated category was composed of eels for which age was determined but, because of their small size, had a high probability of being undifferentiated. Bars and data points are centered at the midpoints of 20-mm length-classes. Sample sizes are in parentheses.

assumptions about apportioning sex made previously (see Methods) are reasonable, the overall ratio of males: females in the Aparima River samples was about 67.9:1. The sexed and apportioned females were evenly distributed among reaches throughout the catchment (Figure 5) but were mostly found in tributaries (Figure 6), especially the smaller tributaries.

Undifferentiated longfin eels (100–139 mm) were mostly found in the lower reaches of the main stem of the catchment (Figures 5, 6). Eels in that size-class had already been in freshwater 1–4 years (Figure 4), showing that movement upriver is slow.

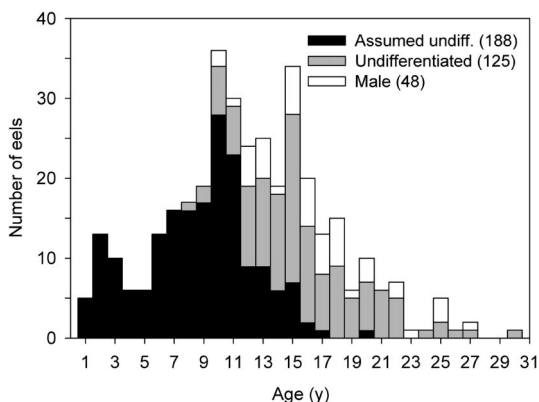


FIGURE 3.—Age frequencies of New Zealand longfin eels from the Aparima River catchment, classified as undifferentiated or male. The assumed undifferentiated category was composed of eels for which age was determined but, because of their small size, had a high probability of being undifferentiated. Sample sizes are in parentheses.

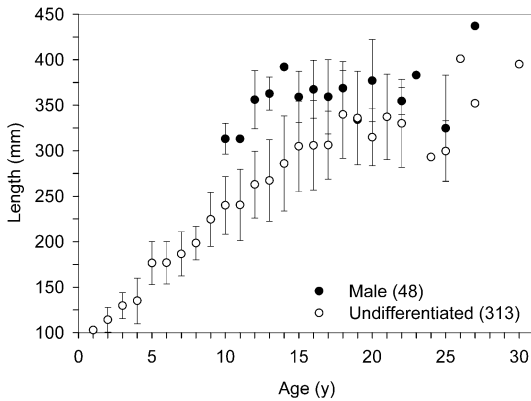


FIGURE 4.—Mean lengths and standard deviations (error bars) at age for the New Zealand longfin eels of Figure 3 (the Aparima River catchment), showing that faster-growing eels of a particular age were more likely to be differentiated than the slower growing eels. Sample sizes are in parentheses.

Only a few eels in that size-class had penetrated to the middle reaches. The change from a skewed and bimodal length distribution in the lower reaches to more symmetrical ones upstream and in the tributaries is further evidence for the slow movement up the catchment. Undifferentiated longfin eels at their modal size of about 290 mm in tributaries and upper reaches (Figures 5, 6) had probably taken 10–20 years to reach those locations (Figure 4), assuming a gradual, unidirectional upstream movement.

Male longfin eels were distributed throughout the catchment. Further, their size distributions were similar throughout the catchment, except that the distributions in the lower reaches and main stem were sharply truncated at the upper ends, a little above the minimum legal commercial size (Figures 5, 6).

There was a low representation of longfin eels 140–400 mm in the samples (Figures 5, 6), but this was probably because of sampling bias rather than rarity of these sizes in the population. Although electric fishing and fyke netting sampled various habitats, effort was not equal between methods or among habitats, and both electric fishing and especially fyke netting are size-selective (Figure 7). Many smaller eels could have escaped through the mesh of the fyke nets. Both sampling methods revealed the sharp decline at the upper ends of the length-frequency distributions.

Shortfin Eel Sex Ratio and Distribution

Of 31 shortfin eels that were gonadally differentiated in the Aparima catchment, 26 were fe-

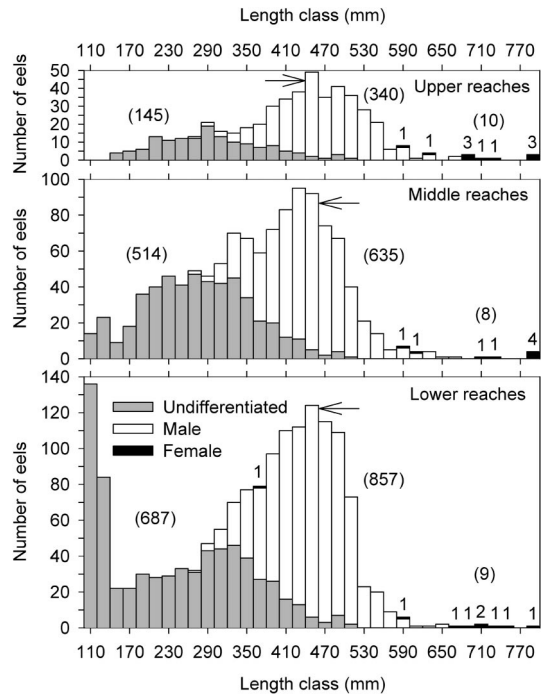


FIGURE 5.—Length-frequencies of New Zealand longfin eels from the lower, middle, and upper reaches of the Aparima River catchment that were classified as undifferentiated, male, or female. All measured eels are included. Those not examined for sex were assigned a sex, based on the proportions of the sexes of those examined in each length-class and the assumption that any unexamined eels greater than 680 mm long were female. Bars are centered at the midpoints of 20-mm length-classes. Arrows mark the size-class at entry into the commercial fishery. Numbers above bars are the numbers of females. Sample sizes in parentheses.

males, in distinct contrast to the high male: female ratio among longfin eels. However, shortfin eels were rare in the samples, being outnumbered by longfin eels 27:1 (Table 2).

Shortfin eels were distributed differently than longfin eels, shortfin eels being relatively more abundant in the estuary and in low-reach and middle-reach tributaries. In those locations, the longfin eel: shortfin eel ratios in the catches were between 5:1 and 13:1, whereas the overall ratio in the main stem was 86:1 (Table 2). Shortfin eels actually outnumbered longfin eels in two middle-reach tributaries.

The 34 shortfin eels greater than 540 mm, which were determined or presumed to be females (Beentjes and Chisnall 1998; Beentjes 1999), plus 15 shorter eels sexed as females, were more highly represented in the estuary and lower main stem

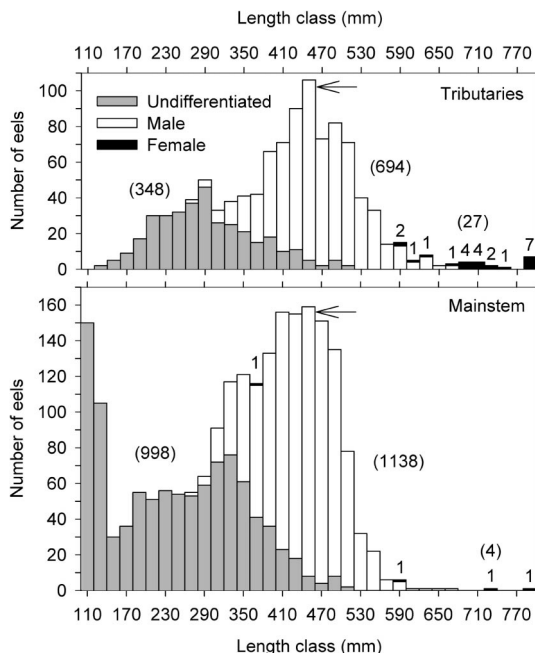


FIGURE 6.—Length-frequencies of New Zealand longfin eels from the main stem (lower panel) and tributaries (upper panel) of the Aparima River catchment that were classified as undifferentiated, male, or female. Those not examined for sex were assigned a sex, based on the proportions of the sexes of those examined in each length-class and the assumption that any unexamined eels greater than 680 mm long were female. Bars are centered at the midpoints of 20-mm length-classes. Arrows mark the size-class at entry into the commercial fishery. Numbers above bars are the numbers of females. Sample sizes in parentheses. The data include the eels depicted in Figure 5.

than were undifferentiated or shorter unexamined shortfin eels (Table 2). Of the five identified as males, two were at the middle tributary site, where the largest catch of shortfin eels was made, one was at an upper tributary site, and two were at a lower main-stem site.

Discussion

Identification of Female Eels

Because of the unexpected extreme male predominance in the Aparima River population of longfin eels, the possibility arises that female longfin eels were misidentified as males, or simply classified as undifferentiated juveniles. In this study, about 50% of the 340–360-mm longfin eels were classified as males (Figure 2), which is near the lowest size reported to be developing males (Todd (1974). However, it is unlikely that many eels were

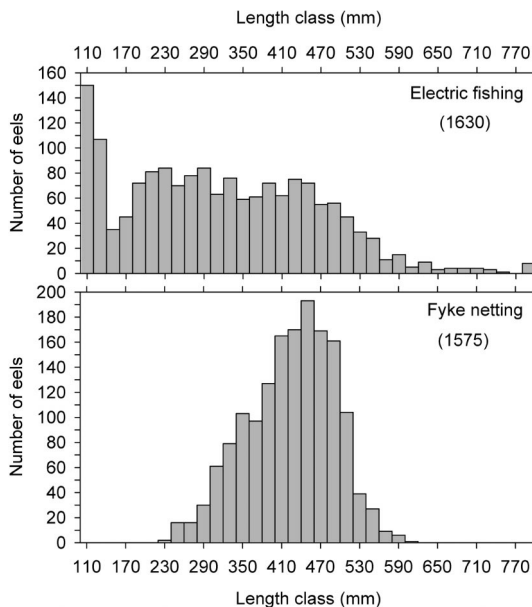


FIGURE 7.—Length-frequencies of New Zealand longfin eels from the Aparima River catchment captured by electric fishing (upper panel) and by fyke netting (lower panel). Sample sizes in parentheses.

misclassified because we carefully followed Todd’s (1974) comprehensive descriptions and diagrams of developing gonadal stages for both longfin eels and shortfin eels. Nevertheless, our assumption that unexamined longfin eels longer than 680 mm were females might have resulted, if anything, in a only a slight overestimate of the proportion of females in the population.

TABLE 2.—Relative abundance of shortfin eels in the Aparima River catchment, New Zealand, shown as the ratio of New Zealand longfin eels to shortfin eels (sexes combined) and the minimum percentage of female shortfin eels in the total number of shortfin eels. The actual numbers of shortfin eels are in parentheses and are the same for the bottom section, so they are not repeated there.

Stream category	Reach			Total
	Lower	Middle	Upper	
Relative abundance of shortfin eels				
Estuary	5:1 (14)			5:1 (14)
Main stem	52:1 (23)	851:1 (1)	28:0 (0)	86:1 (24)
Tributaries	13:1 (23)	6:1 (48)	42:1 (11)	13:1 (82)
Total	26:1 (60)	24:1 (49)	45:1 (11)	27:1 (120)
Relative abundance of female shortfin eels				
Estuary	71.4			71.4
Main stem	56.5	0.0		54.2
Tributaries	39.1	29.2	27.3	31.7
Total	53.3	28.6	27.3	40.8

TABLE 3.—Ratios of male to female (M:F) New Zealand longfin eels in the commercial catches from South Island rivers, New Zealand, sampled in fishing seasons of 1996–1997 and 1997–1998 (data from Beentjes and Chisnall 1998; Beentjes 1999).

River	M:F ratio	Sample size
Southernmost five major rivers		
Waiau	2.4:1	675
Aparima	13.6:1	774
Aparima (scientific) ¹	67.9:1	1,859
Oreti	4.6:1	1,448
Mataura ²	4.8:1	1,462
Clutha	3.2:1	1,381
Headwaters		
Taieri ³	0.2:1	348
Waikaka Stream ⁴	0.01:1	86
Other rivers		
Waitaki	1.1:1	619
Eight others combined	0.4:1 to 2.0:1	46–226

¹ Including those apportioned as male and female.

² Excluding Waikaka Stream.

³ Above Taieri River gorge.

⁴ Headwater stream of the Mataura River.

Skewed Sex Ratios in Southern South Island Rivers

The preponderance of male longfin eels in the present electric fishing and fyke netting samples (68:1; Figures 5, 6) was consistent with the commercial fyke-netted catch from the Aparima River (Table 3). Combining the two summer fishing seasons of 1996–1997 and 1997–1998, the male: female ratio was 14:1 ($N = 774$; data from Beentjes and Chisnall 1998; Beentjes 1999). The actual ratio, however, was probably higher because about 50% of the commercial catch was reported as undifferentiated ($N = 782$). In our study, sex was determined for more than 95% of longfin eels in the commercial size range.

The preponderance of male longfin eels also occurred in other rivers in the southern half of the South Island, although the Aparima River was the extreme. In the five large, southernmost catchments, the ratio of males to females in the commercial catches ranged from 2.4:1 to 13.6:1 (Table 3; Beentjes and Chisnall 1998; Beentjes 1999). Because of the conservative assignment of sex by those authors, the actual ratios were probably higher. Approximately three-quarters of the South Island longfin eel catch is produced by those five catchments (Beentjes and Bull 2002). In the headwaters of the southern Taieri River, only recently accessible to commercial fishing, the catch was predominated by females (0.2:1). The male: female ratios of longfin eels in commercial catches

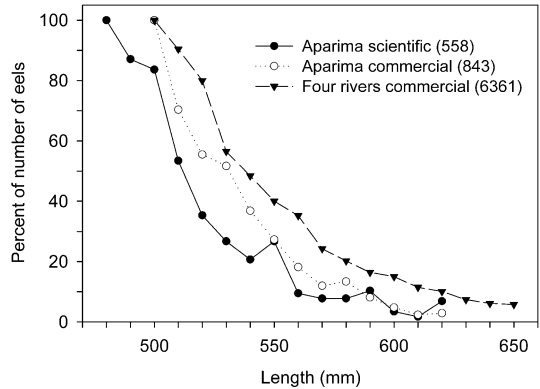


FIGURE 8.—Percentages of number of New Zealand longfin eels in the smallest length-class (such that the smallest length-class will equal 100%) and in succeeding 10-mm modal length-classes, as depicted for scientific samples and commercial catches in the Aparima River and in the commercial catches in four other southern South Island catchments, New Zealand. The starting length-class for the scientific samples was a secondary mode, chosen to approximate the commercial catch modes. Commercial catch data are from Beentjes and Chisnall (1997) and Beentjes (1999). Four rivers commercial includes the Waiau, Oreti, Mataura, and Clutha rivers combined. Sample sizes in parentheses.

from nine other rivers in more northerly parts of the South Island ranged from 0.4:1 to 2.0:1 (Table 3), though sample sizes were small for most.

In contrast, the commercial catch of shortfin eels in all South Island rivers was nearly 100% female (Beentjes and Chisnall 1998; Beentjes 1999). Only 6 of 1,153 shortfin eels sampled in the catches from the five southernmost rivers were males. Most male shortfin eels mature and migrate to sea at a size smaller than the minimum legal size (220 g, about 470 mm; Todd 1980; Jellyman and Todd 1998; Francis and Jellyman 1999).

Truncated Size Distributions in Southern South Island Rivers

The truncated length-frequency distributions of longfin eels in the Aparima River (this study) and other South Island rivers (Beentjes and Chisnall 1998; Beentjes 1999) are considered to be a consequence of an intense and sustained commercial eel fishery. The rapid decline in numbers of longfin eels greater than 500 mm in the scientific samples from the Aparima River was mirrored in the commercial catches from the Aparima River and from four other major southern rivers (Figure 8). Rapid decline in proportion of the catch for eels exceeding the minimum legal size (220 g, about 460 mm)

shows that baited fyke nets used in the commercial fishery are quite effective in harvesting longfin eels. Much larger eels were common before and in the early stages of commercial fishing (Cairns 1942; Burnet 1952; Beentjes and Chisnall 1997).

In a recent study, unbaited fyke nets were used to sample longfin eels in Lee Stream, a headwater tributary of the Taieri River, at sites with easy or difficult access to commercial fishers (T. L. Broad, University of Otago, personal communication). The length-frequency distribution of eels at the difficult sites was normal, whereas that at the easy sites was significantly nonnormal and truncated sharply above 600 mm. The mean length of eels was significantly greater (by 60 mm) at the difficult sites. Similarly, Broad et al. (2001) found longfin eels sampled by electric fishing at different sites in the Lee Stream catchment to be significantly longer at difficult than at easy access sites.

The length-frequency of shortfin eels harvested by the commercial fishery in southern rivers decreased more gradually with increasing size above the minimum legal limit. The modal length of shortfin eels in the commercial catch for the five southernmost rivers combined was 580 mm, whereas it was only 500 mm for longfin eel, despite the fact that the longfin eel is a much larger species. In the southern rivers, longfin eels are targeted with baited fyke nets, to which shortfin eels respond less readily. It may be that the rarer shortfin eels in those rivers are less vulnerable to commercial fishing.

Where shortfin eels are targeted by a commercial fishery, the same reduction in size distribution and truncation occurs, often abruptly. In the 3 years after the beginning of a commercial fishery in one South Island lagoon, the mean length of eels in scientific samples had declined by 100 mm (Jellyman 1993). Only about 10% of the eels in the second sample exceeded the mean length of the first sample.

Historical Sex and Size Distributions in Southern Rivers

Both the sex ratios and length distributions have changed with time in the major southern South Island rivers, although directly comparable studies have not been conducted. Cairns (1941) ironically suggested a campaign of eel destruction and stated, "Eleven thousand eels were taken from the Hedgehope River . . . in Southland. These were all long-finned females." The Hedgehope River is a tributary of the Oreti River, 20 km east of the Aparima River. Above the head of tide in the Oreti

River, ". . . all samples consisted of long-finned female eels. This was also true for . . . the Aparima River and the Waiau River." The 11,624 eels (all caught in baited traps of unspecified mesh or mouth size) in the Hedgehope River and its tributaries in the lower Oreti catchment had an average weight of 1.22 kg (Cairns 1942). A longfin eel of that weight would have been approximately 780 mm long (Hoyle and Jellyman 2002) and female. Longfin eels in the commercial catch in the Oreti catchment in 1996–1998 averaged only 516 mm (Beentjes and Chisnall 1998; Beentjes 1999).

Burnet (1952) caught longfin eels in baited traps with 25-mm-diameter mesh in tributaries of the Waiau River. The 606 eels also averaged 780 mm, whereas the recent commercial catch averaged 536 mm. From Burnet's length composition table, 48% were greater than 760 mm and certainly female, and 72% were greater than 690 mm and probably more than 95% female.

Harries (1974) collected longfin eels in the Clutha catchment with baited traps and in the Taieri River catchment by electric fishing and with baited traps. Females were much more abundant than males among the eels for which sex could be determined. In the Clutha River 87% were female ($N = 85$) and in the Taieri River 78% were female ($N = 282$).

Commercial fishing in the southern rivers became significant in the early 1970s (Beentjes and Chisnall 1997). Data from commercial eel processors shows that the proportion of longfin eels in smaller weight categories increased markedly between the 1970s and the 1990s.

A significant decline in catch per unit effort for longfin eels also occurred in the rivers of the southern half of the South Island through the period 1991–1999 (Beentjes and Bull 2002). For the Southland Region, where earlier data are comparable, the 1990s continued a declining trend observed in the 1980s (Jellyman 1993). Changing sex ratio and fishing down of large females over time probably have contributed to the declining catch per unit effort.

Why are Sex Ratios Skewed toward Males in Southern Rivers?

Given the predominance of female longfin eels in the southern rivers before commercial fishing (Cairns 1941, 1942; Burnet 1952), what has caused the change to a predominance of males, especially in the Aparima River? Three possibilities are considered here; of course, the cause might be a combination of factors. (1) The selective commercial

harvest of larger, longer-lived females created truncated size distributions with an associated skew of expressed sex ratios. If so, potential sex ratios would still be at preharvest values, and elimination of harvest would allow the sex ratios to return to preharvest values over time. (2) Commercial harvest has restructured the river populations such that biotic environmental conditions (e.g., social interactions) now favor the development of males. If so, elimination of commercial harvest might not produce a return to preharvest values or a return to those values might take much longer. (3) Other environmental features of the catchments, natural or anthropogenic, have changed to favor the development of males. If so, elimination of the commercial harvest would have no direct effect on sex ratios, other than allowing the few females in the population the chance to reproduce.

Two lines of argument suggest that the observed sex ratio in the Aparima River and other southern rivers was not just a simple function of harvesting. Commercial fishing does cause a rapid drop in longfin eel numbers just exceeding the legal size limit. However, it apparently does not skew the sex ratio within a given size-class. First, among the eels between about 440 and 560 mm in our samples (Figure 6), we found few undifferentiated eels and therefore little potential to increase female numbers. At the lower end of this size range, the population has not yet been directly affected by fishing. Developing females, certainly at the upper end of that size range, should have been recognizable had they been present. Only a few in that size range were recognized by Beentjes (1999) from samples taken 3 or 4 years earlier.

Second, a simple modeling exercise showed that although commercial fishing increases the rate of decline in numbers of eels above the legal size, it does not alter the sex ratio *per se*. Previously used values of growth rate (13 mm/year), natural mortality rate (0.04/year), and probability of male migration as a function of size for longfin eels (Francis and Jellyman 1999; Hoyle and Jellyman 2002) were combined with a sexual differentiation schedule for males approximated from Figure 2 via a logistic equation. A similar schedule was used for females but at a larger size range. A fishing mortality of 0.1/year was superimposed gradually over 5 years on the natural mortality rate. It was assumed that an individual in a length-cohort of undifferentiated eels had equal potential to become male or female.

In the model, males greatly outnumbered fe-

males at smaller sizes because males become recognizably differentiated earlier than females. The sex ratio gradually changed with increasing eel length to approximate 1:1 at lengths where all eels are differentiated, whether fishing occurred or not. The ratio then trended toward female predominance because males matured and emigrated earlier than females.

It seems more likely that changed factors in the environment caused differentiation of a greater proportion of the population into males in the last 2 decades than in earlier decades. Those eels in our samples identified as males (mostly 300–600 mm) would have entered the Aparima catchment between the early 1970s or 1980s for the larger males and the early 1990s for the smaller males, and depending on growth rates: assumed 13 mm/year (our study) or 23 mm/year (Beentjes and Chisnall 1998; Beentjes 1999). It is not known at what size environmental factors exert their influence on sex determination, but the influence is probably well before differentiated testes are discernable.

As a result, we could not determine whether the factors influencing differentiation relate to commercial fishing or to other aspects of the environment. Commercial fishing does alter the size structure of the population. For example, between the mid-1970s and the mid-1990s the proportion by weight of longfin eels greater than 710 mm fell from 60% to 32% in the catch handled by the largest South Island eel processor (Beentjes and Chisnall 1997) and has probably fallen further since. Almost all longfin eels greater than 710 mm are females. A reduced proportion of large eels in the southern river populations might have allowed a greater survival rate of smaller eels (e.g., through reduced cannibalism or competition for food). A consequent increase in population density of small eels might have favored differentiation of males (e.g., Parsons et al. 1977; Kennedy and Vickers 1990; Krueger and Oliveira 1999). The perceived increased population density might be exaggerated, if the reduction of large eels resulted in increased encounter rates among smaller eels. Large longfin eels altered the daytime resting habitat preferences of smaller longfin eels in experimental conditions (Glova 2001), but the behavioral influence of large eels on smaller ones during nighttime is unknown. Large eels may inhibit the nighttime emergence of smaller eels from within the substrate, which would reduce the encounter rates and perhaps allow differentiation of females.

Low electric fishing catches of longfin eels 150–

230 mm (Figure 7) are evidence that some years of low recruitment occurred in the Aparima River, although the electric fishing was not a random sample of all habitats available to eels. If the low catches reflect actual low density of small eels, the argument just presented would be countered, but most of the males we sampled would have differentiated before the period of low recruitment. Unfortunately, there are no historical records of density of eels less than legal size against which to compare current density.

It is also possible that the presence of large females inhibits the differentiation of males through chemical communication. The glass eel stage of the European and American eels respond behaviorally to exceedingly low concentrations of substances from other eels and other aquatic animals (e.g., amino acids; Sola et al. 1993; Sola and Tongiorgi 1998) and bile salts (Sola and Tosi 1993). Reactions of glass eels to conspecific yellow eels and their bile are equivocal (Miles 1968; Pesaro et al. 1981; Sorensen 1986). Apparently, the possible influence of pheromones on sexual differentiation has not been studied in eels.

Climatic factors, particularly temperature and precipitation, have changed in recent decades, but it seems unlikely that the slight trends could have caused the dramatic shift in sex ratio. Compared with the 2 decades preceding 1950, air temperatures over Southland have since warmed (Salinger and Mullan 1999), increasing about 0.14°C per decade (Wratt and Salinger 2001), but with substantial interannual variation. Holmgren (1996) showed a slight increase in percentage of cultured European eels that became males with elevated temperature, but only with constant culture temperatures of 6°C or more apart. In Southland, annual precipitation between 1976 and 1994 averaged about 10% above the long-term average (1930–1994; Salinger and Mullan 1999; Wratt and Salinger 2001). This small change is overshadowed by the normal range of flow variation from dry to wet periods of 1–2 orders of magnitude in the Aparima catchment (Robertson 1992).

Anthropogenic changes to the environment have also occurred in the Aparima and other Southland and Otago catchments. Many of these have been gradual since the mid-1980s, such as conversion of forest to pasture and cropland. The most obvious change in land use in the Aparima catchment, coinciding in part with the changes in eel population structure, has been the rapid increase in dairy farming and consequent increase in nutrient loading in some areas of the catchment.

Clearing and livestock grazing have reduced riparian cover and increased the erosion of shingle into the upper part of the catchment, causing greater instability of the riverbed (Robertson 1992). Although such changes gradually alter the general characteristics of the water courses, they do not affect the entire catchment simultaneously, whereas the change in eel population structure apparently is catchmentwide.

In summary, commercial fishing selectively harvests female longfin eels, but does not, per se, account for lack of immature females smaller than legal size. The climatic and anthropogenic changes to the environment evident in the southern South Island seem to have been more gradual and on different time scales than the changes in eel sex ratio in the Aparima River and nearby rivers. Commercial fishing has altered the size structure of the eel population, probably altering the social structure, such that differentiation into males has been enhanced. The perceived increase in density of small eels may be the driving factor.

Implications for Conservation and Management

The conservation and management of highly exploited, highly fecund, pelagic-spawning marine fishes is difficult at best. For highly fecund marine teleost fishes, it is theoretically unlikely that spawning stock-recruitment relationships can be defined because of the high variability in density-independent and density-dependent mortality rates (Koslow 1992). For longfin eels, it is also practically unlikely because there are no means to assess the spawning stock; the spawning area is only conjecture (Jellyman 1987).

Koslow (1992) attributed the supposed resilience of such teleosts to exploitation to the production of large numbers of small eggs. However, Sadovy (2001) rejected the argument that fecundity, per se, offers resilience to exploitation, suggesting that it is inappropriate to compare the tiny eggs of a high fecundity broadcast spawner with those of a low-fecundity producer of yolk-filled eggs. Sadovy (2001) cited the families Scorpaenidae, Serranidae, and Sciaenidae as examples of marine fishes that have not been protected from exploitation by their high fecundity. Common features of these are longevity, delayed sexual maturity, sporadic recruitment, and iteroparity. Reproductive potential of species in all these families, and in anguillids, is also reduced by the harvest of juveniles. To further complicate the issue, recruitment variation in marine fishes increases with fecundity (Rickman et al. 2000) and longevity

(Longhurst 2002), when taxonomic relatedness is taken into account.

These and related ideas have been developed for iteroparous species having wholly marine life cycles. Can they be applied to conservation of longfin eels and other anguillids that have an unusual catadromous life cycle with semelparity? Semelparity obviously worked in an evolutionary sense long before there was commercial fishing, even for a geographically restricted endemic species, the longfin eel. Before fishing, a comparatively extended age at maturity and single-time spawning were counterbalanced by the fact that large female longfin eels were top predators and food generalists in New Zealand fresh waters and experienced a low mortality rate.

Anguillids have a long larval life with high mortality, which is probably density-independent because of their rarity in the sea (Kleckner and McCleave 1988; Tesch and Wegner 1990). This is followed by a period of years in fresh waters during which mortality and sexual differentiation are partly or largely density-dependent, and during which sex-related size dimorphism at maturity develops. Anguillids share characteristics (other than iteroparity) with other exploited marine pelagic spawners: longevity and delayed sexual maturity (Todd 1980; Vøllestad 1992; Chisnall and Hicks 1993; Jellyman 1995; Svedäng et al. 1996; Oliveira and McCleave 2000), high fecundity (Todd 1981; Barbin and McCleave 1997), and probably variable recruitment in an unexploited state. In that state, the presence of many age-classes in the annual spawning migration from a river (Vøllestad and Jonsson 1986; Oliveira and McCleave 2000) and across the continental range (Vøllestad and Jonsson 1986; Vøllestad 1992) achieves the same outcome as the bet-hedging strategy of iteroparity in non-anguillids.

Truncation of the size and age distribution of female longfin eels tends to negate that outcome in two ways. First, fewer age classes and fewer total spawners probably contribute to increased recruitment variability, where recruitment refers to glass eels entering fresh waters. Secondly, reduced mean size of spawning females reduces the potential fecundity disproportionately because fecundity is an exponential function of length: about L^4 in the longfin eel (Todd 1981) and about L^3 in the American eel (Barbin and McCleave 1997). “[F]ecundity is an inappropriate criterion for identifying extinction risk” (Sadovy 2001), especially for an endemic species with restricted geographic range. The transformation of important female-

producing rivers into male-predominated rivers exacerbates the direct size truncation problem from commercial fishing.

Conventional management practices are inappropriate and ineffective for the anguillid-type life cycle. The maximum size limit on longfin eels on the South Island (4 kg), or even one much smaller, as instituted to protect a portion of the females, serves little pragmatic function because eels are vulnerable to the fishery for so many years that few if any reach that size (Hoyle and Jellyman 2002). The minimum legal size, 220 g, was instituted on the basis of yield-per-recruit and marketability considerations. The minimum size does little good as a conservation measure because in heavily exploited rivers a large percentage is caught as they recruit to legal size. A female has to grow to 10× the minimum weight to have a 5% chance of maturing and migrating (calculated from relations in Hoyle and Jellyman 2002). The present quota management system for the South Island provides a cap on harvest. However, it is ineffective as a management tool because it is not applied by species, and it does not protect females, which are still vulnerable for many more years than males. Management to date has presupposed that small females carry through to maturity, but evidence presented here does not support that supposition.

Freshwater reserves for eels, where eel fishing would be prohibited, were proposed during the early stages of the developing commercial fishery in New Zealand by Castle (1972), who warned then of a possible crisis unless thought be given to the long-term consequences of ever-increasing wild eel harvest. The call for reserves in relatively unfished rivers has been repeated (Hoyle and Jellyman 2002). However, the unfished or lightly fished areas do not appear to have protected the integrity of the eel population to date. Most of these areas are unproductive, as reflected in slow eel growth, and the total area is small and inadequate (Jellyman 1993) compared with the total exploited area. To be effective, additional reserves would be needed (Hoyle and Jellyman 2002), perhaps many more (Clark 1996).

Two actions are needed urgently, one a conservation or management action and the other a research action. First, the fishery needs to be restructured or substantially curtailed, such that increased numbers of females are allowed to mature and migrate to sea. Options are available, and more than one may be necessary, though they may be painful to commercial interests. Legal designation of re-

serves is one. Converting the fishery from its focus on yellow eels to a focus on migrating silver eels would allow a maximum size to be set so that some or all females could escape the fishery. Transfer of elvers or undifferentiated yellow eels to waters where eels are rare or absent is another option, though this would have to be done in a manner favoring differentiation into females, not males. Secondly, on a longer term, the environmental factors determining sexual differentiation need to be elucidated so further conservation actions might be taken to restore populations in rivers that were historically female.

If short-term changes are not instituted, the application of research results may never come to fruition. The time is now to invoke the precautionary principle.

Acknowledgments

E. Graynoth, who directed the wider Aparima River study, provided advice through the present research. M. L. Bonnett, G. R. Kelly, and J. R. E. Sykes assisted with eel collection. C. Buard and G. R. Kelly aged the eels. J. R. E. Sykes and G. R. Kelly prepared Figure 1. V. Thompson (Mossburn Enterprises) loaned us fyke nets. J. D. M. was a visiting scientist at the National Institute of Water and Atmospheric Research while this research was conducted. The study was partly funded by the Foundation for Research, Science and Technology (New Zealand), contract NO1X003, and the Ministry of Fisheries, Contract EEL2001/O2.

References

- Avise, J. C., G. S. Helfman, N. C. Saunders, and L. S. Hales. 1986. Mitochondrial DNA differentiation in North Atlantic eels: population genetic consequences of an unusual life history pattern. *Proceedings of the National Academy of Sciences* 83:4350–4354.
- Barbin, G. P., and J. D. McCleave. 1997. Fecundity of the American eel *Anguilla rostrata* at 45° N in Maine, U.S.A. *Journal of Fish Biology* 51:840–847.
- Bastrop, R., B. Strehlow, K. Jürss, and C. Sturmbauer. 2000. A new molecular phylogenetic hypothesis for the evolution of freshwater eels. *Molecular Phylogenetics and Evolution* 14:250–258.
- Beentjes, M. P. 1999. Size, age, and species composition of commercial eel catches from South Island market sampling, 1997–98. NIWA Technical Report 51. National Institute of Water and Atmospheric Research, Wellington, New Zealand.
- Beentjes, M. P., and B. Bull. 2002. CPUE analyses of the commercial freshwater eel fishery. New Zealand Fisheries Assessment Report 2002/18. Ministry of Fisheries, Wellington, New Zealand.
- Beentjes, M. P., and B. L. Chisnall. 1997. Trends in size and species composition and distribution of commercial eel catches. New Zealand Fisheries Data Report 89. National Institute of Water and Atmospheric Research, Wellington, New Zealand.
- Beentjes, M. P., and B. L. Chisnall. 1998. Size, age, and species composition of commercial eel catches from market sampling, 1996–97. NIWA Technical Report 29. National Institute of Water and Atmospheric Research, Wellington, New Zealand.
- Boubée, J. A., C. P. Mitchell, B. L. Chisnall, D. W. West, E. J. Bowman, and A. J. Haro. 2001. Factors regulating the downstream migration of mature eels (*Anguilla* spp.) at Aniwhenua Dam, Bay of Plenty, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 35:121–134.
- Broad, T. L., C. R. Townsend, G. P. Closs, and D. J. Jellyman. 2001. Microhabitat use by longfin eels in New Zealand streams with contrasting riparian vegetation. *Journal of Fish Biology* 59:1385–1400.
- Burnet, A. M. R. 1952. Studies on the ecology of the New Zealand long-finned eel, *Anguilla dieffenbachii* Gray. *Australian Journal of Marine and Freshwater Research* 3:32–63.
- Cairns, D. 1941. Life-history of the two species of New Zealand fresh-water eel, part I. Taxonomy, age and growth, migration, and distribution. *New Zealand Journal of Science and Technology* 23:53B–72B.
- Cairns, D. 1942. Life-history of the two species of fresh-water eel in New Zealand. III. Development of sex. Campaign of eel destruction. *New Zealand Journal of Science and Technology* 23:173B–178B.
- Castle, P. H. J. 1972. Prospects for the New Zealand freshwater eel industry. *Commercial Fishing* 11:13–15.
- Chan, I. K. K., D. K. O. Chan, S. C. Lee, and K. Tsukamoto. 1997. Genetic variability of the Japanese eel *Anguilla japonica* (Temminck & Schlegel) related to latitude. *Ecology of Freshwater Fish* 6:45–49.
- Chisnall, B. L., and B. J. Hicks. 1993. Age and growth of longfinned eels (*Anguilla dieffenbachii*) in pastoral and forested streams in the Waikato River basin, and in two hydro-electric lakes in the North Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 27:317–332.
- Chisnall, B. L., and C. Kemp. 2000. Size, age, and species composition of commercial eel catches from market sampling in the North Island, 1997–98. NIWA Technical Report 87. National Institute of Water and Atmospheric Research, Wellington, New Zealand.
- Clark, C. W. 1996. Marine reserves and the precautionary management of fisheries. *Ecological Applications* 6:369–370.
- Colombo, G., and R. Rossi. 1978. Environmental influences on growth and sex ratio in different eels populations (*Anguilla anguilla* L.) of Adriatic coasts. Pages 313–320 in D. S. McLusky and A. A. Berry, editors. *Physiology and Behaviour of Marine Organisms*. Pergamon, Oxford.
- De Leo, G. A., and M. Gatto. 1996. Trends in vital rates

- of the European eel: evidence for density dependence. *Ecological Applications* 6:1281–1294.
- Duncan, M. J. 1992. Flow regimes of New Zealand rivers. Pages 13–27 in M. P. Mosley, editor. *Waters of New Zealand*. New Zealand Hydrological Society, Wellington.
- Egusa, S. 1979. Notes on the culture of the European eel (*Anguilla anguilla* L.) in Japanese eel-farming ponds. *Rapports et Procès-verbaux des Réunions Conseil international pour l'Exploration de la Mer* 174:51–58.
- Francis, R. I. C. C., and D. J. Jellyman. 1999. Are mean size data adequate to monitor freshwater eel fisheries? *Marine and Freshwater Research* 50:355–366.
- Glova, G. J. 2001. Effects of the presence of subadult longfinned eels (*Anguilla dieffenbachii*) on cover preferences of juvenile eels (*Anguilla* spp.) in replicate channels. *New Zealand Journal of Marine and Freshwater Research* 35:221–233.
- Glova, G. J., D. J. Jellyman, and M. L. Bonnett. 2001. Spatiotemporal variation in the distribution of eel (*Anguilla* spp.) populations in three New Zealand lowland streams. *Ecology of Freshwater Fish* 10:147–153.
- Graynoth, E. 1999. Improved otolith preparation, ageing and back-calculation techniques for New Zealand freshwater eels. *Fisheries Research* 42:137–146.
- Guerrero, III, R. D., and W. L. Shelton. 1974. An acetocarmine squash method for sexing juvenile fishes. *Progressive Fish-Culturist* 36:56.
- Harries, D. H. A. 1974. Sex, growth and distribution of the longfinned eel, *Anguilla dieffenbachii*. M. S. thesis, University of Otago, Dunedin, New Zealand.
- Holmgren, K. 1996. Effect of water temperature and growth variation on the sex ratio of experimentally reared eels. *Ecology of Freshwater Fish* 5:203–212.
- Hoyle, S. D., and D. J. Jellyman. 2002. Longfin eels need reserves: modelling the effects of commercial harvest on stocks of New Zealand eels. *Marine and Freshwater Research* 53:887–896.
- Hu, L. C., and P. R. Todd. 1981. An improved technique for preparing eel otoliths for aging. *New Zealand Journal of Marine and Freshwater Research* 15:445–446.
- Jellyman, D. J. 1987. Review of the marine life history of Australasian temperate species of *Anguilla*. *American Fisheries Society Symposium* 1:276–285.
- Jellyman, D. J. 1993. A review of the fishery for freshwater eels in New Zealand. *New Zealand Freshwater Research Report* 10. National Institute of Water and Atmospheric Research, Christchurch, New Zealand.
- Jellyman, D. J. 1995. Longevity of longfinned eels *Anguilla dieffenbachii* in a New Zealand high country lake. *Ecology of Freshwater Fish* 4:106–112.
- Jellyman, D. J., G. J. Glova, P. M. Sagar, and J. R. E. Sykes. 1997. Spatio-temporal distribution of fish in the Kakanui River estuary, South Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 31:103–118.
- Jellyman, D. J., and P. R. Todd. 1998. Why are migrating male shortfinned eels (*Anguilla australis*) in Lake Ellesmere, New Zealand, getting smaller but not younger? *Bulletin Francais de la Pêche et de la Pisciculture* 349:141–152.
- Jessop, B. M. 1987. Migrating American eels in Nova Scotia. *Transactions of the American Fisheries Society* 116:161–170.
- Kennedy, G. J. A., and K. U. Vickers. 1990. The fish of Lough Neagh. Part B. Investigations on salmon (*Salmo salar* L.) and eels (*Anguilla anguilla* L.) in the lower River Bann. Pages 397–417 in R. B. Wood and R. V. Smith, editors. *Lough Neagh*. Kluwer Academic, Dordrecht.
- Kleckner, R. C., and J. D. McCleave. 1988. The northern limit of spawning by Atlantic eels (*Anguilla* spp.) in the Sargasso Sea in relation to thermal fronts and surface water masses. *Journal of Marine Research* 46:647–667.
- Koslow, J. A. 1992. Fecundity and the stock-recruitment relationship. *Canadian Journal of Fisheries and Aquatic Sciences* 49:210–217.
- Krueger, W. H., and K. Oliveira. 1999. Evidence for environmental sex determination in the American eel, *Anguilla rostrata*. *Environmental Biology of Fishes* 55:381–389.
- Lintas, C., J. Hirano, and S. Archer. 1998. Genetic variation of the European eel (*Anguilla anguilla*). *Molecular Marine Biology and Biotechnology* 7:263–269.
- Longhurst, A. 2002. Murphy's law revisited: longevity as a factor in recruitment to fish populations. *Fisheries Research* 56:125–131.
- McDowall, R. M. 1990. *New Zealand freshwater fishes: a natural history and guide*. Heinemann Reed, Auckland.
- McDowall, R. M. 1993. Implications of diadromy for the structuring and modeling of riverine fish communities in New Zealand. *New Zealand Journal of Marine and Freshwater Research* 27:453–462.
- McDowall, R. M. 1998. Fighting the flow: downstream-upstream linkages in the ecology of diadromous fish faunas in West Coast New Zealand rivers. *Freshwater Biology* 40:111–122.
- Miles, S. G. 1968. Rheotaxis of elvers of the American eel (*Anguilla rostrata*) in the laboratory to water from different streams in Nova Scotia. *Journal of the Fisheries Research Board of Canada* 25:1591–1602.
- Naismith, I. A., and B. Knights. 1990. Modelling of unexploited and exploited populations of eels, *Anguilla anguilla* (L.), in the Thames Estuary. *Journal of Fish Biology* 37:975–986.
- Oliveira, K., and J. D. McCleave. 2000. Variation in population and life history traits of the American eel, *Anguilla rostrata*, in four rivers in Maine. *Environmental Biology of Fishes* 59:141–151.
- Oliveira, K., J. D. McCleave, and G. S. Wipphausser. 2001. Regional variation and the effect of lake:river area on sex distribution of American eels. *Journal of Fish Biology* 58:943–952.
- Parent, S., and L. M. Schriml. 1995. A model for the determination of fish species at risk based upon life-

- history traits and ecological data. *Canadian Journal of Fisheries and Aquatic Sciences* 52:1768–1781.
- Parsons, J., K. U. Vickers, and Y. Warden. 1977. Relationship between elver recruitment and changes in the sex ratio of silver eels *Anguilla anguilla* L. migrating from Lough Neagh, Northern Ireland. *Journal of Fish Biology* 10:211–229.
- Pesaro, M., M. Balsamo, G. Gandolfi, and P. Tongiorgi. 1981. Discrimination among different kinds of water in juvenile eels, *Anguilla anguilla* (L.). *Monitore Zoologica Italiana* 15:183–191.
- Rickman, S. J., N. K. Dulvy, S. Jennings, and J. D. Reynolds. 2000. Recruitment variation related to fecundity in marine fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 57:116–124.
- Robertson, B. M. 1992. Aparima catchment water quality review. Report to Southland Regional Council. Barry Robertson and Associates, Dunedin, New Zealand.
- Roncarati, A., P. Melotti, O. Mordenti, and L. Gennari. 1997. Influence of stocking density of European eel (*Anguilla anguilla*, L.) elver on sex differentiation and zootechnical performances. *Journal of Applied Ichthyology* 13:131–136.
- Sadovy, Y. 2001. The threat of fishing to highly fecund fishes. *Journal of Fish Biology* 59(supplement A): 90–108.
- Salinger, M. J., and A. B. Mullan. 1999. New Zealand climate: temperature and precipitation variations and their links with atmospheric circulation 1930–1994. *International Journal of Climatology* 19: 1049–1071.
- Sang, T.-K., H.-Y. Chang, C.-T. Chen, and C.-H. Hui. 1994. Population structure of the Japanese eel, *Anguilla japonica*. *Molecular Biology and Evolution* 11:250–260.
- Smith, P. J., P. G. Benson, C. Stanger, B. L. Chisnall, and D. J. Jellyman. 2001. Genetic structure of New Zealand eels *Anguilla dieffenbachii* and *A. australis* with allozyme markers. *Ecology of Freshwater Fish* 10:132–137.
- Sola, C., A. Spampinato, and L. Tosi. 1993. Behavioural responses of glass eels (*Anguilla anguilla*) towards amino acids. *Journal of Fish Biology* 42:683–691.
- Sola, C., and P. Tongiorgi. 1998. Behavioural responses of glass eels of *Anguilla anguilla* to non-protein amino acids. *Journal of Fish Biology* 53:1253–1262.
- Sola, C., and L. Tosi. 1993. Bile salts and taurine as chemical stimuli for glass eels, *Anguilla anguilla*: a behavioural study. *Environmental Biology of Fishes* 37:197–204.
- Sorensen, P. W. 1986. Origins of the attractant(s) of migrating elvers of the American eel, *Anguilla rostrata*. *Environmental Biology of Fishes* 17:185–200.
- Svedäng, H., E. Neuman, and H. Wickström. 1996. Maturation patterns in female European eel: age and size at the silver eel stage. *Journal of Fish Biology* 48:342–351.
- Tesch, F.-W., and G. Wegner. 1990. The distribution of small larvae of *Anguilla* sp. related to hydrographic conditions 1981 between Bermuda and Puerto Rico. *Internationale Revue der gesamten Hydrobiologie* 75:845–858.
- Todd, P. R. 1974. Studies on the reproductive biology of New Zealand freshwater eels. Doctoral dissertation. Victoria University of Wellington, Wellington.
- Todd, P. R. 1980. Size and age of migrating New Zealand freshwater eels (*Anguilla* spp.). *New Zealand Journal of Marine and Freshwater Research* 14:283–293.
- Todd, P. R. 1981. Hormone-induced maturation in male New Zealand freshwater eels (*Anguilla* spp.). *New Zealand Journal of Marine and Freshwater Research* 15:237–246.
- Vøllestad, L. A. 1992. Geographic variation in age and length at metamorphosis of maturing European eel: environmental effects and phenotypic plasticity. *Journal of Animal Ecology* 61:41–48.
- Vøllestad, L. A., and B. Jonsson. 1986. Life-history characteristics of the European eel *Anguilla anguilla* in the Imsa River, Norway. *Transactions of the American Fisheries Society* 115:864–871.
- Wirth, T., and L. Bernatchez. 2001. Genetic evidence against panmixia in the European eel. *Nature (London)* 409:1037–1040.
- Wratt, D., and J. Salinger. 2001. Past climate variations over New Zealand. National Institute of Water and Atmospheric Research. Available: <http://www.niwa.co.nz/rc/atmos/clivar/pastclimate>. (January 2003).