

Prey selection and dietary overlap of shortfinned (*Anguilla australis*) and longfinned (*A. dieffenbachii*) eels during summer in the Horokiwi Stream, New Zealand

P. M. SAGAR

E. GRAYNOTH

G. J. GLOVA

National Institute of Water and Atmospheric
Research Limited
P.O. Box 8602
Christchurch, New Zealand
email: psagar@niwa.co.nz

Abstract Benthic macroinvertebrates were collected and the diets of shortfinned eels (*Anguilla australis*) and longfinned eels (*Anguilla dieffenbachii*) inhabiting a small coastal New Zealand stream were examined to investigate intraspecific and interspecific trophic partitioning and prey selection. Our results showed intraspecific segregation of preferred prey among three size classes of juvenile shortfinned eels, but there was significant overlap between different size classes of longfinned eels. All size classes of both species of eel fed nocturnally on similar prey, and so there was no indication of temporal or trophic segregation. Therefore, habitat separation is assumed to be the main mechanism to reduce interspecific competition in these two co-occurring species of eels.

Keywords diel feeding; competition; trophic partitioning; Anguillidae

INTRODUCTION

Following a review of resource partitioning in fish assemblages, Ross (1986) concluded that unlike terrestrial ecosystems, trophic separation is more important than habitat separation in fish communities, with temporal partitioning of resources being least important. He also found that the degree

of relatedness of fish affected the level at which resource partitioning occurred, with habitat or trophic partitioning more important the more closely related the fish taxa. In addition, for many fish there are major ontogenetic shifts in feeding (Ross 1978; Livingston 1982; Werner 1986), and so competition and predation may occur between different sizes of the same species.

In New Zealand, populations of the closely related shortfinned eels (*Anguilla australis* Richardson) and longfinned eels (*Anguilla dieffenbachii* Gray) frequently dominate freshwater fish communities (Glova et al. 1985; Hayes et al. 1989; Sagar & Glova 1994). Glass eels of both species arrive from the ocean and enter fresh water during July–December (Jellyman 1977a), at c. 60–70 mm total length (TL) and then become resident in estuaries and lower rivers before undertaking further upstream migration (Jellyman 1977b). Upstream migration usually ceases when the eels are 250–350 mm TL (Jellyman 1979). Eventually, habitat separation occurs, with shortfinned eels usually predominating in lowlands and not usually penetrating as far upstream as longfinned eels (McDowall 1990).

Despite their predominance in freshwater fish communities, only Glova et al. (1998) determined the relative importance of habitat variables on the distribution of both species of eel. However, factors affecting their distribution and abundance were reported by Hayes et al. (1989), Hanchet (1990), and Jowett et al. (1996) and their habitat preferences by Jowett & Richardson (1995) and Jellyman et al. (2003).

The diet of eels in New Zealand rivers has been the subject of several studies. For example, of the extent of their predation on introduced salmonids (e.g., Cairns 1942), of the inter-relationships between the diets of eels and brown trout *Salmo trutta* (Burnet 1952, 1969), and of the diets of eels and other co-existing fish species (Hopkins 1965, 1970; Cadwallader 1975; Sagar & Eldon 1983; Sagar & Glova 1994). Studies of the food items and feeding habits of eels in lakes include those of Ryan (1984, 1986) and Jellyman (1989). Sagar & Glova (1998)

compared the timing of feeding and prey selection of three size classes of shortfinned eel in a New Zealand river. However, of all these studies only Jellyman (1989) and Sagar & Glova (1998) compared diets over a wide range of sizes. Consequently, relatively little is known about the overlap in prey preferences and potential competition for food resources of overlapping populations of the two species of eel.

In the present study the diets of shortfinned and longfinned eels co-occurring in a single, short stretch of stream were examined. The primary objectives were to examine diets of all sizes of both eel species to determine: (1) prey selectivity; and (2) possible differences in dietary composition with size and species of eels. These objectives were used to test the hypotheses that trophic partitioning of resources occurred: (1) intraspecifically, between eels of different size; and (2) interspecifically, between the two co-occurring, closely related species of eels. Previously, Sagar & Glova (1998) showed that shortfinned eels of all sizes feed predominantly from post-dusk to dawn. Consequently, sampling of eels during the present study was restricted to a similar period and stomach content samples from larger eels (>350 mm TL) were obtained by lavage, so that the number of eels killed were kept to a minimum.

STUDY AREA AND METHODS

Field sampling

This study was carried out in the Horokiwi Stream (catchment area 3302 ha), a lowland stream north of Wellington, New Zealand. The study area (41°06'S, 174°54'E) was in the middle reaches of the Horokiwi Stream, where the wetted area was 8–10 m wide with grasses (*Poa* spp.) and some willows (*Salix* spp.) and pines (*Pinus* spp.) growing on steep banks. A more detailed physical description of the Horokiwi Stream can be found in Glova et al. (1998), and Jellyman et al. (2000) provide an assessment of changes in fish habitat in the stream over a 50-year period. Sampling was completed over a 500-m-long section of stream comprising mainly shallow runs and riffles with a few small, shallow pools. The bed of the study area varied between 100 mm and 400 mm depth and comprised loosely arranged gravel (90%) and small cobble (10%) in the riffles and runs, with sand in the few shallow pools. During this study the flow of the stream was c. 0.2 m³s⁻¹ and water temperatures, as measured from a hand-held thermometer accurate to

±0.5°C, ranged from 20°C at 1800 h to 17°C at 0015 h. There had been small freshes (with discharges of up to 5.0 m³s⁻¹) on 1 and 7 November 1999 (P. M. Sagar unpubl. data), but these had not disturbed the streambed, as we observed periphyton on the substrate. During sampling, water levels were 50–100 mm above normal and some marginal grasses were submerged, but the water was clear.

Five sets of samples of eels were collected at 1.0–1.5 h intervals between 1720 h and 0740 h New Zealand Standard Time (NZST), 9–10 November 1999. Sunset occurred at 1908 h and sunrise at 0502 h (NZST), and the night was cloudy and without moonlight.

Eels were stunned by means of a pulsed DC backpack electro-shocker and collected from the stream. To avoid disturbing eels for subsequent collections, for each set of eel samples, sampling progressed in an upstream direction, with a minimum of 10 m of unsampled stream between sets. Electric fishing disturbs benthic invertebrates, which may enter the drift, and move downstream with the flowing water (Fowles 1975). Consequently, sampling in an upstream direction should avoid disturbing invertebrates so that they become available to feeding fish. Eels, anaesthetised with a mild dose of 2-phenoxyethanol, were measured to the nearest 1.0 mm TL on a standard measuring board and weighed to the nearest 5 g on a top-loaded electronic balance. Those eels 90–350 mm TL were then placed in separate containers and killed with a strong dose of 2-phenoxyethanol before preservation in 4% formaldehyde. Laboratory experiments showed that using the lavage method (where a pump was used to flush water into the stomachs of larger eels, thereby dislodging any food items, which were then regurgitated by the eels), 90–95% of food items could be flushed from the stomachs of eels >350 mm TL (E. Graynoth unpubl. data). Consequently, the lavage method was used to obtain the stomach contents of eels >350 mm TL and these eels were returned alive to a section of the stream downstream of the sampling area. The stomach contents of each eel that was lavaged were stored separately and preserved in 4% formaldehyde.

To determine the relationship between food consumed and food available, 10 benthic macro-invertebrate samples were collected from randomly selected locations within the study area before eel sampling began. Benthic samples were collected with a Waters & Knapp (1961) sampler (area 0.097 m²) fitted with a 350-µm mesh. All samples were preserved in the field in 1.6% formaldehyde.

Laboratory procedures

In the laboratory, the stomach of each eel was removed. Stomach and lavage samples were examined for food contents under a stereomicroscope. Freshly eaten food items (those prey which were intact and showed little indication of digestion) were separated and identified to the lowest practical taxon before being counted. These freshly eaten food items were considered to be representative of the diet of the eel species, although some variation in digestion rates of the different taxa was likely. This method was most likely to underestimate the relative proportions of soft-bodied taxa (e.g., oligochaetes and free-living trichopterans) and overestimate those with external cases (e.g., gastropods and cased trichopterans) or sclerotised parts (e.g., ephemeropterans and plecopterans) (MacDonald et al. 1982). Partly digested and digested remains were retained in a separate category and no effort was made to determine the proportions of the different prey taxa among them. Benthic macroinvertebrate samples were identified to the lowest practical taxon, and counted.

Data analyses

Sagar & Glova (1998) showed that there was considerable overlap in the diet of shortfinned eels 101–200 mm and 201–300 mm TL, with less overlap between these two size classes and those <101 mm TL. In the present study only four eels <101 mm TL were captured, and so eels of each species were assigned to one of the following size classes: <201 mm, 201–300 mm, and >300 mm TL.

The extent of prey selection was examined by Ivlev's (1961) index (E) for the major prey items:

$$E = (R_i - P_i)/(R_i + P_i)$$

where R_i is the proportion of taxon i in the diet and P_i is its proportion in the benthos. Values can range

from 1.0 for high selection to -1.0 for complete avoidance. Dietary overlap (α) between fish species was calculated by the method of Schoener (1970):

$$\alpha = 1 - 0.5(\sum^n P_{xi} - P_{yi})$$

where P_{xi} is the proportion of prey type i in the diet of species x , P_{yi} is the proportion of prey type i in the diet of species y , and n is the number of prey types. An overlap of 0.6 or greater was considered significant in this study.

Measurements of the TL of each eel species were compared for sampling period by the application of t tests (Zar 1984); size differences were considered significant if $P < 0.05$.

RESULTS

Eels

All eels (60 shortfinned and 126 longfinned) were found and collected from marginal vegetation or open gravel and cobbles adjacent to the stream banks. Within species the mean sizes of eels were similar between sampling occasions, but between species longfinned eels were longer than shortfinned eels on each sampling occasion (Table 1).

Nocturnal feeding patterns

Too few eels were collected to discern any variation in nocturnal feeding by size class. Therefore nocturnal feeding patterns were assessed for all size classes combined, by species.

Overall, the numbers of freshly eaten prey in the stomachs of both species (Fig. 1) increased throughout the night and were greatest immediately before dawn (0502 h), which indicates feeding throughout the hours of darkness. However, there were differences in the timing of feeding of both

Table 1 Sampling times, sizes (total length, mm) and proportions of shortfinned eels *Anguilla australis* and longfinned eels *A. dieffenbachii* with empty stomachs from the Horokiwi Stream, Wellington, New Zealand, 9–10 November 1999. (n , denotes sample size; t and P refer to the results of t tests between the sizes of the two species of eels for each time period.)

Species: NZST (h)	Shortfinned eel				Longfinned eel				t	P
	n	Mean \pm SE	Range	% empty	n	Mean \pm SE	Range	% empty		
1720–1900	14	175 \pm 67	87–342	14.3	23	302 \pm 128	133–599	43.5	5.42	<0.001
2000–2230	11	146 \pm 67	97–314	36.4	33	279 \pm 123	87–551	15.2	3.86	<0.001
2325–0210	12	188 \pm 65	115–299	50.0	32	339 \pm 125	105–563	3.1	4.56	<0.001
0330–0450	10	176 \pm 84	99–374	10.0	22	251 \pm 130	123–562	0	1.66	NS
0620–0740	13	212 \pm 82	109–338	38.5	16	291 \pm 113	166–509	12.5	1.07	NS

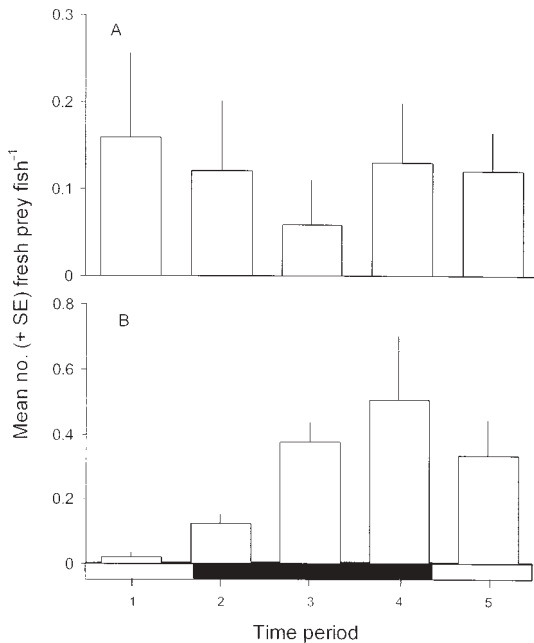


Fig. 1 Numbers (mean + SE) of fresh prey per stomach for **A**, shortfinned eels *Anguilla australis*; and **B**, longfinned eels *A. dieffenbachii* sampled on five occasions in the Horokiwi Stream, New Zealand, 9–10 November 1999. The solid bar on the x axis indicates the period of darkness. Time periods: 1, 1720–1900 h; 2, 2000–2230 h; 3, 2325–0210 h; 4, 0330–0450 h; 5, 0620–0740 h.

species. In longfinned eels the numbers of freshly eaten prey in the stomachs increased as the night progressed until about dawn and then decreased. However, in shortfinned eels there was an initial increase in the number of prey consumed at dusk and then numbers declined until c. 0300 h when the numbers of consumed prey increased again. In addition, for longfinned eel the proportion of eels with empty stomachs decreased as night progressed (Table 1). However, among shortfinned eels there was no pattern of a declining proportion of fish with empty stomachs with time of night (Table 1).

Benthos and diets of eels

Chironomids, the amphipod *Paracalliope fluviatilis*, and oligochaetes made up c. 56%, 13%, and 11% of the benthos, respectively. Blackflies *Austrosimulium* spp., the purse-cased caddisfly *Oxyethira albiceps*, gastropod *Potamopyrgus antipodarum*, free-living caddisflies Hydrobiosidae, net-spinning caddisflies *Aoteapsyche* spp., and coleopterans *Hydora* sp. were

the only other taxa to comprise >1% of the benthos (Table 2).

Aquatic invertebrates were eaten by eels of all three size classes and both species, although the proportions of the different prey taxa consumed varied (Table 2). In addition, the number of invertebrate taxa eaten varied with size class and species. Among shortfinned eels, small fish ate nine taxa, and fish in the medium and large size classes ate seven taxa. However, among longfinned eels, small fish ate six taxa whereas fish of both medium and large size classes ate 10 taxa. *Paracalliope fluviatilis* comprised a major proportion of the diet of all three size classes of both species of eels. In addition, *Austrosimulium* larvae comprised a major proportion of the diet of small-sized eels of both species and medium-sized longfinned eels. *Potamopyrgus antipodarum* comprised an important proportion of the diet of large-sized longfinned eels, and was of increasing importance with increasing size of shortfinned eels. The high proportion of Arachnida in the diet of medium-sized shortfinned eels resulted from the selective feeding of one fish only that had consumed all 84 mites recorded in this analysis.

Prey of terrestrial origin were taken only occasionally, with an adult dipteran being consumed by a small shortfinned eel and adult dipterans, a centipede and wood lice being consumed by longfinned eels (Table 2).

Prey selection and dietary overlaps

Within both species of eel, all three size classes showed distinct prey preferences. The prey selection indices (Table 3) indicate that among shortfinned eels the amphipod *P. fluviatilis* was eaten preferentially by all three size classes. In addition, the gastropods *P. antipodarum* and *Physa* sp. were eaten preferentially by medium- and large-sized eels, larvae of the cased caddisfly *Pycnocentrodus* sp. and free-living caddisflies *Hydrobiosis* spp. were preferred by small- and large-sized eels, and small-sized eels preferentially consumed nematodes and *Austrosimulium* larvae. Oligochaetes and larvae of the purse-cased caddisfly *O. albiceps* and chironomids were under-represented in the diets of all three sizes classes of shortfinned eel. In addition, *P. antipodarum* was under-represented in the diet of small eels; nematodes, *Hydrobiosis* spp., *Pycnocentrodus* sp., and *Austrosimulium* spp. were under-represented in the diets of medium-sized eels; and nematodes and *Austrosimulium* spp. were under-represented in the diets of large eels. Among longfinned eels, *P. fluviatilis* was eaten preferentially by all three size

classes. In addition, *Austrosimulium* larvae were preferred by small- and medium-sized eels; nematodes and *Physa* sp. by medium- and large-sized eels; and *P. antipodarum* by large eels. Oligochaetes, *O. albiceps*, and chironomid larvae were under-represented in the diets of all size classes; and *P. antipodarum* and *Pycnocentroides* spp. were under-represented in the diets of small- and medium-sized eels.

Among shortfinned eels, there was no significant overlap in the diets of the three size classes (small:medium $\alpha = 0.318$; small:large $\alpha = 0.389$; medium:large $\alpha = 0.534$). In contrast, the diets of medium- and large-sized and small- and medium-sized longfinned eels overlapped significantly ($\alpha = 0.723$ and $\alpha = 0.618$ respectively), but there was less overlap in the diets of small and large eels ($\alpha = 0.400$). Between species of eels, the diets of small-

Table 2 Relative abundance (%) of macroinvertebrates in the benthos and prey in the diets of small (<201 mm), medium (201–300 mm), and large (>300 mm) *Anguilla australis* and *A. dieffenbachia*, in the Horokiwi Stream, Wellington, New Zealand, 9–10 November 1999. Numbers of eels of each size class containing fresh prey are given in parentheses. (–, not present; *, <0.1%.)

Taxon	Benthos	<i>A. australis</i>			<i>A. dieffenbachia</i>		
		Small (20)	Medium (9)	Large (3)	Small (23)	Medium (30)	Large (46)
Aquatic							
Oligochaeta	11.0	0.8	0.5	–	0.4	0.4	0.4
Bivalvia	–	–	–	–	–	–	–
<i>Pisidium</i> sp.	–	2.5	–	–	–	–	–
Gastropoda	–	–	–	–	–	–	–
<i>Physa</i> sp.	–	–	2.1	1.3	–	0.5	4.2
<i>Potamopyrgus antipodarum</i>	3.2	2.5	4.7	7.7	–	1.2	24.4
Ostracoda	–	–	1.0	–	–	0.1	0.1
Amphipoda	–	–	–	–	–	–	–
<i>Paracalliope fluviatilis</i>	13.0	26.2	44.8	79.5	27.4	59.9	56.9
Hemiptera	–	–	–	–	–	–	0.1
Megaloptera	–	–	–	–	–	–	–
<i>Archicauliodes diversus</i>	0.2	–	–	–	–	0.1	*
Plecoptera	0.8	–	–	–	0.2	–	*
Ephemeroptera	–	–	–	–	–	–	–
<i>Deleatidium</i> spp.	–	2.6	–	–	0.4	0.3	0.1
Odonata	–	–	0.5	–	–	–	–
Trichoptera	–	–	–	–	–	–	–
<i>Aoteapsyche</i> spp.	1.4	–	–	1.3	–	–	*
<i>Hydrobiosis</i> spp.	1.9	6.6	0.5	3.8	1.5	1.8	2.1
<i>Hudsonema</i> sp.	–	–	–	–	–	–	*
<i>Pycnocentroides</i> sp.	0.4	1.6	–	1.3	–	0.3	0.4
<i>Pycnocentria evecta</i>	–	–	–	–	–	–	*
<i>Oecetis unicolor</i>	–	–	–	–	–	–	0.1
<i>Oxyethira albiceps</i>	4.2	3.3	–	–	0.8	3.6	0.6
Coleoptera	–	–	–	–	–	–	–
<i>Hydora</i> sp.	2.0	–	–	–	–	0.1	*
Diptera	–	–	–	–	–	–	–
<i>Austrosimulium</i> spp.	5.4	39.3	–	1.3	61.3	25.2	4.4
Chironomidae	55.7	13.1	2.1	3.8	6.1	6.1	5.6
Muscidae	–	–	–	–	–	–	0.1
Tipulidae	0.1	–	–	–	–	–	0.1
Arachnida	0.2	–	43.8	–	–	–	*
Terrestrial							
Isopoda	–	–	–	–	0.2	0.1	0.1
Myriopoda	–	–	–	–	–	–	0.1
Diptera	*	0.8	–	–	1.7	–	*
Total no.	2440	122	192	78	525	1113	5074

($\alpha = 0.755$) and medium- ($\alpha = 0.741$) sized fish overlapped significantly, but there was less overlap in the diets of large eels ($\alpha = 0.496$).

DISCUSSION

Our results showed that all sizes of both shortfinned eels and longfinned eels fed at night and that, by size, there was no significant overlap in diet within shortfinned eels, but significant overlap within different sizes of longfinned eels. In addition, the diets of similar-sized eels of both species were similar.

In New Zealand, nocturnal activity of eels is well documented. If activity of eels is assumed to indicate feeding, then Ryan (1984) found shortfinned eels to be active primarily at night in a coastal lake. Likewise, Glova & Jellyman (2000) found that all individuals up to 299 mm TL of both species of eels were nocturnally active in a laboratory stream, and Sagar & Glova (1998) found that the most fresh prey items in the stomachs of shortfinned eels collected from one stream occurred at night. In the present study, the number of fresh food items in the stomachs of shortfinned eels peaked about dusk and just before dawn, a bimodal pattern similar to that found by Sagar & Glova (1998). These results might indicate a crepuscular feeding pattern. Similarly, Ryan (1984) found that in Lake Ellesmere the fullness values of the stomachs of large shortfinned eels increased throughout the night, with greatest values about dawn. The nocturnal feeding times of longfinned eels are not so well determined. However, Glova & Jellyman (2000) determined that in an experimental stream, juvenile longfinned eels were significantly more active during the night than shortfinned eels.

Such activity patterns could explain the differences in feeding found in the present study, where the number of fresh prey in the stomachs of longfinned eels increased steadily throughout the night, whereas numbers in shortfinned eel stomachs had a bimodal pattern of occurrence.

Our results showed that there was no significant overlap in composition of the diet of shortfinned eels of different sizes. All three size classes of shortfinned eels showed preferences for aquatic macroinvertebrates, which other studies have shown to account for the majority of food items eaten (e.g., Cairns 1942; Burnet 1952, 1969; Hopkins 1965; 1970; Cadwallader 1975; Ryan 1986; Jellyman 1989; Sagar & Glova 1998). Gastropods such as *P. antipodarum* and *Physa variabilis* have been consistently reported as major components of the diet of larger (>350 mm TL) shortfinned eels in rivers (e.g., Burnet 1969; Hopkins 1970; Cadwallader 1975; Sagar & Glova 1998) and lakes (e.g., Ryan 1986; Jellyman 1989). However, gastropods were under-represented in the diets of smaller (<200 mm TL) shortfinned eels (Jellyman 1989; Sagar & Glova 1998; this study). In contrast, the cased caddisflies *Pycnocentroides* spp. were almost completely avoided by all size classes of shortfinned eels in a previous study (Sagar & Glova 1998), but in the present study they were consumed preferentially. The diet of longfinned eels, however, was similar between all size classes, although gastropods were, as with shortfinned eels, a major component of the diet of the large and medium sizes, and were generally under-represented in the diet of small longfinned eels.

The absence of fish from the diet of the larger longfinned eels is of interest. Although the diet of longfinned eels <350 mm TL has been reported to

Table 3 Prey selection, examined by Ivlev's (1961) index, as calculated from the numbers of invertebrates in each of the main prey categories in the diets of three size classes of *Anguilla australis* and *A. dieffenbachii* in relation to those found in the benthos, Horokiwi Stream, Wellington, New Zealand, 9–10 November 1999.

Taxon	<i>A. australis</i>			<i>A. dieffenbachii</i>		
	Small (<200 mm)	Medium (201–300 mm)	Large (>300 mm)	Small (<200 mm)	Medium (201–300 mm)	Large (>300 mm)
Oligochaeta	-0.86	-0.91	-1.00	-0.93	-0.93	-0.93
<i>Potamopyrgus antipodarum</i>	-0.12	0.19	0.41	-1.00	-0.45	0.77
<i>Physa</i> sp.	0.00	1.00	1.00	0.00	1.00	1.00
<i>Paracalliope fluviatilis</i>	0.34	0.56	0.72	0.36	0.64	0.63
<i>Hydrobiosis</i> spp.	0.55	-0.58	0.33	-1.00	-0.14	0.00
<i>Pycnocentroides</i> sp.	0.60	-1.00	0.53	-1.00	-0.14	0.00
<i>Oxyethira albiceps</i>	-0.12	-1.00	-1.00	-0.68	-0.08	-0.75
<i>Austrosimulium</i> spp.	0.76	-1.00	-0.61	0.84	0.65	-0.10
Chironomidae	-0.62	-0.93	-0.87	-0.80	-0.80	-0.82

comprise almost solely invertebrate prey (e.g., Cadwallader 1975; Sagar & Eldon 1983), larger eels have been found to feed to an increasing extent on bullies (*Gobiomorphus* spp.) and juvenile brown trout (*S. trutta*) so that these prey comprise a significant proportion of the diet of eels >700 mm TL (e.g., Cadwallader 1975; Jellyman 1996). The absence of fish in the diet of the large longfinned eels that we sampled could be explained by the low density of brown trout in the Horokiwi Stream during 1996 (Jellyman et al. 2000). Shortfinned eels >500 mm TL feed extensively on fish (Ryan 1986), but we did not sample any individual of this species >374 mm TL, so that the absence of fish in the diet was not unusual. In addition, although no density data are available for the Horokiwi Stream, the biomass of native fish species other than eels during 1996 was considered to be insignificant (Jellyman et al. 1996).

We found that the diet of similar sized shortfinned and longfinned eels overlapped, particularly between the small and medium size classes. Consequently, resource segregation of juvenile longfinned and shortfinned eels in the Horokiwi Stream did not occur through trophic differences or temporal differences in foraging activity. Therefore, habitat segregation appears to be the most important mechanism to ameliorate interspecific competition. Such segregation has been demonstrated in the wild by Glova et al. (1998), who found that juvenile longfinned eels tended to associate with faster water velocities and larger substrates of riffles, whereas shortfinned eels occupied slower, marginal habitats. These habitat preferences were corroborated by Glova (1999), who found that in artificial channels juvenile longfinned eels tended to occupy cobbles associated with riffles whereas shortfinned eels preferred the cover of macrophytes in slower, marginal sections. Likewise, in a study of the daytime habitat of longfinned and shortfinned eels in four New Zealand rivers, Jellyman et al. (2003) found marked interspecific differences in habitat preferences, although the differences were more apparent for larger eels than smaller eels.

In general, our hypotheses were only partly supported by the results of the present study. Ontogenetic shifts in diet were identified for shortfinned eels, but not longfinned eels over the size ranges of fish sampled. Hard-bodied prey, such as the gastropods *P. antipodarum* and *Physa* sp., made up a greater proportion of the diet of large and medium than small shortfinned eels. The diet of longfinned eels indicated a similar, but less strong,

trend towards larger eels consuming a greater proportion of hard-bodied prey. There was considerable overlap in diet between longfinned and shortfinned eels of similar size, which indicated no major interspecific differences in prey selectivity. Consequently, in the Horokiwi Stream there appears to be no separation of the timing of foraging activity and main prey of longfinned and shortfinned eels.

ACKNOWLEDGMENTS

We gratefully acknowledge the assistance of Marty Bonnett and Mark Taylor in the field sampling. Don Jellyman provided constructive comments on an earlier draft of the manuscript. The study was funded by the New Zealand Foundation for Science, Research and Technology, contract no. CO1X0006.

REFERENCES

- Allen KR 1951. The Horokiwi Stream: a study of a trout population. New Zealand Marine Department Fisheries Bulletin 10: 1–238.
- Burnet AMR 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.
- Burnet AMR 1969. A study of the inter-relation between eels and trout, the invertebrate fauna and the feeding habits of the fish. New Zealand Marine Department, Fisheries Technical Report 36: 1–23.
- Cadwallader PL 1975. Feeding relationships of galaxiids, bullies, eels and trout in a New Zealand river. Australian Journal of Marine and Freshwater Research 26: 299–316.
- Cairns D 1942. Life-history of the two species of freshwater eel in New Zealand. II. Food and inter-relationships with trout. New Zealand Journal of Science and Technology 23: 132–148.
- Fowles CR 1975. Effects of electric fishing on the invertebrate fauna of a New Zealand stream. New Zealand Journal of Marine and Freshwater Research 9: 35–43.
- Glova GJ 1999. Cover preference tests of juvenile shortfinned eels (*Anguilla australis*) and longfinned eels (*A. dieffenbachii*) in replicate channels. New Zealand Journal of Marine and Freshwater Research 33: 193–204.
- Glova G, Jellyman DJ 2000. Size-related differences in diel activity of two species of juvenile eel (*Anguilla*) in a laboratory stream. Ecology of Freshwater Fish 9: 210–218.

- Glova GJ, Bonnett ML, Docherty CR 1985. Comparison of fish populations in riffles of three braided rivers of Canterbury, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 19: 157–165.
- Glova GJ, Jellyman DJ, Bonnett ML 1998. Factors associated with the distribution and habitat of eels (*Anguilla* spp.) in three New Zealand lowland streams. *New Zealand Journal of Marine and Freshwater Research* 32: 255–269.
- Hanchet SM 1990. Effects of land use on the distribution and abundance of native fishes in tributaries of the Waikato River in the Hakarimata Range, North Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 24: 159–171.
- Hayes JW, Leathwick JR, Hanchet SM 1989. Fish distribution patterns and their association with environmental factors in the Mokau River catchment, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 23: 171–180.
- Hopkins CL 1965. Feeding relationships in a mixed population of freshwater fish. *New Zealand Journal of Science* 8: 149–157.
- Hopkins CL 1970. Some aspects of the bionomics in a brown trout nursery stream. *New Zealand Marine Department, Fisheries Research Bulletin* 4: 1–38.
- Ivlev VA 1961. *Experimental ecology of the feeding of fishes*. New Haven, Connecticut, Yale University Press. 302 p.
- Jellyman DJ 1977a. Invasion of a New Zealand freshwater stream by glass-eels of two *Anguilla* spp. *New Zealand Journal of Marine and Freshwater Research* 11: 193–209.
- Jellyman DJ 1977b. Summer upstream migration of juvenile freshwater eels in New Zealand. *New Zealand Journal of Marine and Freshwater Research* 11: 61–71.
- Jellyman DJ 1979. Upstream migration of glass-eels (*Anguilla* spp.) in the Waikato River. *New Zealand Journal of Marine and Freshwater Research* 13: 13–22.
- Jellyman DJ 1989. Diet of two species of freshwater eel (*Anguilla* spp.) in Lake Pounui. *New Zealand Journal of Marine and Freshwater Research* 23: 1–10.
- Jellyman DJ 1996. Diet of longfinned eels, *Anguilla dieffenbachii*, in Lake Rototoi, Nelson Lakes, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 30: 365–369.
- Jellyman DJ, Glova GJ, Bonnett ML, McKerchar AI, Allen KR 2000. The Horokiwi Stream 50 years on: a study of the loss of a productive trout fishery. NIWA Technical Report 83. 50 p.
- Jellyman DJ, Bonnett ML, Sykes JRE, Johnstone P 2003. Contrasting use of daytime habitat by two species of freshwater eel (*Anguilla* spp.) in New Zealand rivers. *American Fisheries Society Symposium on the Biology, Management and Protection of Catadromous Eels* 33: 63–78.
- Jowett IG, Richardson J 1995. Habitat preferences of common, riverine New Zealand native fishes and implications for flow management. *New Zealand Journal of Marine and Freshwater Research* 29: 13–23.
- Jowett IG, Richardson J, McDowall RM 1996. Relative effects of in-stream habitat and land use on fish distribution and abundance in tributaries of the Grey River, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 30: 463–475.
- Livingston RJ 1982. Trophic organization of fishes in a coastal seagrass system. *Marine Ecology Progress Series* 7: 1–12.
- MacDonald JS, Waiwood KG, Green RH 1982. Rates of digestion of different prey in Atlantic cod (*Gadus morhua*), ocean pout (*Macrozoarces americanus*), winter flounder (*Pseudopleuronectes americanus*), and American plaice (*Hippoglossoides platessoides*). *Canadian Journal of Fisheries and Aquatic Sciences* 39: 651–659.
- McDowall RM 1990. *New Zealand freshwater fishes: a natural history and guide*. Auckland, Heinemann Reed. 583 p.
- Ross ST 1978. Trophic ontogeny of the leopard sea-robin, *Prionotus scitulus* (Pisces: Triglidae). *Fisheries Bulletin, United States* 76: 225–234.
- Ross ST 1986. Resource partitioning in fish assemblages: a review of field studies. *Copeia* 1986: 352–388.
- Ryan PA 1984. Diet and seasonal activity of the shortfinned eel, *Anguilla australis*, in Lake Ellesmere, Canterbury, New Zealand. *Environmental Biology of Fishes* 11: 229–234.
- Ryan PA 1986. Seasonal and size-related changes in the food of the shortfinned eel, *Anguilla australis*, in Lake Ellesmere, Canterbury, New Zealand. *Environmental Biology of Fishes* 15: 47–58.
- Sagar PM, Eldon GA 1983. Food and feeding of small fish in the Rakaia River, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 17: 213–226.
- Sagar PM, Glova GJ 1994. Food partitioning by small fish in a coastal New Zealand stream. *New Zealand Journal of Marine and Freshwater Research* 28: 429–436.
- Sagar PM, Glova GJ 1998. Diel feeding and prey selection of three size classes of shortfinned eel (*Anguilla australis*) in New Zealand. *Marine and Freshwater Research* 49: 421–428.

- Schoener TW 1970. Nonsynchronous spatial overlap of lizards in patchy environments. *Ecology* 51: 408–418.
- Waters TF, Knapp RJ 1961. An improved bottom sampler. *Transactions of the American Fisheries Society* 90: 225–226.
- Werner EE 1986. Species interactions in freshwater fish communities. In: Diamond J, Case T ed. *Ecological communities*. New York, Harper & Row. Pp. 344–357.
- Zar JH 1984. *Biostatistical analysis*. New Jersey, Prentice Hall.

