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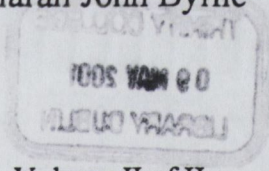
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**The parasite community structure of stocked and wild brown trout
(*Salmo trutta* L.).**

by

Ciaran John Byrne

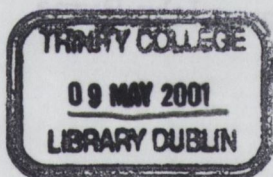


Volume II of II

A thesis submitted in the fulfilment for the Degree of Doctor in Philosophy to Trinity
College, University of Dublin.

October 2000

The parent community structure of stocked and wild brown trout
(Salmo trutta L.).



Thesis
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A thesis submitted in the fulfillment for the Degree of Doctor in Philosophy to Trinity
College, University of Dublin.

October 2000

Chapter 5

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and *A. clavula* in wild and stocked trout in
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5.1 Organisation of chapter five

In chapter five the niches of *P. laevis* and *A. clavula* in the intestine of wild and stocked trout are examined. The niche of *P. laevis* in the intestine of wild trout is first examined for each sample month. The total sample of *P. laevis* is then divided into low, medium and high intensity infections and its distribution in the intestine for each intensity level was examined. The niche width of *P. laevis* in wild trout was then calculated for the total sample, for each sample month and for low, medium and high intensity infections.

P. laevis was examined in stocked trout in the same manner. Its distribution along the intestine was examined for each sample month and when it occurred in low, medium and high intensity infections. The distribution of *P. laevis* in each sample month and in low, medium and high intensity infections was then compared between wild and stocked trout in Lough Feeagh.

The distribution of *A. clavula* was also examined in wild and stocked trout in Lough Feeagh. In both types of trout its distribution was examined for each sample month and when it occurred in low, medium and high intensity infections. The distribution of *A. clavula* was then compared between wild and stocked trout for each sample month and when it occurred in low, medium and high intensity infections.

The Morisita-Horn measure, a quantitative similarity measure was used to calculate the niche overlap values between pairs of the four most prevalent species in wild and stocked trout in Lough Feeagh - *P. laevis*, *A. clavula*, *Crepidostomum farionis* and *E. crassum*. In each case niche overlap values were calculated for the total sample and for each sample month. Niche overlap values for each species pair were then compared between wild and stocked trout.

In the final section of chapter five the distribution of *P. laevis* was examined when it co-occurred with *A. clavula* and *E. crassum* in low, medium and high intensity

infections in wild and stocked trout. Similarly the distribution of *A. clavula* was examined when it co-occurred with *P. laevis* and *E. crassum* in low, medium and high intensity infections in wild and stocked trout. These combinations of parasites were examined in detail as they were considered to be the most likely species to interact in the intestine of trout.

5.2 Examination of the niche of *P. laevis* in the intestine of wild and stocked trout in Lough Feeagh

The niche occupied by the acanthocephalan *P. laevis* in wild and stocked trout in Lough Feeagh was examined in detail. Its distribution along the intestine was calculated for the total sample (both years combined) and for each sample month. Finally, the distribution of *P. laevis* along the length of the intestine was compared between wild and stocked trout.

5.2.1 *P. laevis* in wild trout

The fundamental niche of *P. laevis* along the intestine of wild trout from Lough Feeagh was first examined (Fig 5.1). This sample was divided and the distribution of *P. laevis* was examined for each sample month (Figs 5.2-5.3), and in low, medium and high intensity infections (Fig 5.4).

5.2.2 Total sample of *P. laevis* examined by month

The number of *P. laevis* individuals recorded ranged from 95 in April to 566 in May. 1188 worms were removed from the wild trout sample from Lough Feeagh (Table 5.1; Fig 5.1). The mean percentage position of worms along the intestine decreased from April to November. Median values also decreased from a peak in April to their lowest value in November.

The maximum location value recorded for *P. laevis* along the intestine was 100% and the lowest minimum location value, 29.6%, was recorded in May (Table 5.1). Correspondingly, May also had the largest range of occurrence along the intestine. April had the smallest range of occurrence, with just over 51% of the intestine occupied by *P. laevis*.

Values for the interquartile range were lowest in April and highest in November. 25% quartile values decreased from April to November and 75% quartile values decreased from a peak in May to their lowest level in November (Table 5.1).

All months had negative skewness values, which suggest that in all cases the distribution of *P. laevis* had an asymmetric tail extending towards more negative values. The negatively skewed distribution of *P. laevis* in the intestine of trout in each sample month was unsurprising given the fact that the preferred location for *P. laevis* in the intestine of trout is the posterior portion of the intestine (Kennedy *et al.*, 1978). All months had positive kurtosis values, which suggests that *P. laevis* had a peaked distribution.

One-way analysis of variance (ANOVA) was used to compare the distribution of *P. laevis* along the intestine for each sample month. A significant difference existed in the distribution of *P. laevis* between months for the overall sample (F ratio = 14.2; df = 6, 1181; $p \leq 0.0001$). Least squares difference post hoc tests showed which sample months had significantly different distributions from each other. Of the twenty-one possible paired month combinations (for the seven sample months), fifteen were significantly different from each other. Results are presented in Appendix 2, Table 1.

5.2.3 Total sample of *P. laevis* examined by intensity of infection

Data for the distribution of *P. laevis* were then examined in three groups, low, medium and high, depending upon the number of parasites infecting individual fish. A low intensity infection was when one to five worms infected a fish, medium intensity was when six to nine worms infected a fish and high intensity infection was when ten or more worms infected a fish (Table 5.2; Fig 5.4). The ranges for low, medium and high intensity infections of *P. laevis* although somewhat arbitrary, were established by examining the raw data and constructing frequency histograms.

Of the 1188 worms from the total sample of wild trout, 795 were in high intensity infections, 137 were in medium intensity infections and the remaining 256 were in low intensity infections. The mean position of *P. laevis* along the intestine was lowest for worms in high intensity infections, and highest for worms in medium intensity infections (Table 5.2). The mean positions for worms in low and medium intensity infections were comparable.

Low intensity infections had the lowest median value and medium intensity infections had the highest median value. However, in all cases median values were comparable (Table 5.2). Median values were lower than mean values for low and medium intensity infections. Median values were within the range of values recorded when the total sample was examined by month (Table 5.1).

The lowest minimum position along the intestine was recorded in high intensity infections and the highest minimum position was recorded in low intensity infections (Table 5.2). Thus, the range of occurrence of *P. laevis* along the intestine increased from low to high intensity infections.

Values for the 25% quartile were comparable between low, medium and high intensity infections. 75% quartile values were also comparable between the three groups. Correspondingly, the interquartile range increased from low to high intensity infections (Table 5.2). All three groups had negative skewness values and positive kurtosis values. This would indicate that for low, medium and high intensity infections *P. laevis* had a relatively peaked distribution with an asymmetric tail extending towards more negative values (Table 5.2; Fig 5.4).

One-way analysis of variance (ANOVA) was used to examine the differences in the distribution of *P. laevis* along the intestine between low, medium and high intensity infections. A significant overall difference was found (F ratio = 8.3; $df = 2, 1186$; $p \leq 0.0003$). Least squares difference post hoc tests showed that there were significant differences in the distribution of *P. laevis* between high and low ($p \leq 0.003$) and between high and medium intensity infections ($p \leq 0.0008$). Medium intensity infections had the most posterior mean position, high intensity infections had the most anterior mean position and low intensity infections had an intermediate value.

In a similar manner to chapter three the niche width of *P. laevis* in the intestine of wild trout from Lough Feeagh was calculated using Culver's 1972 standardised Shannon-Wiener function, H' , for the total sample (0.71) and for each sample month

(April = 0.73, May = 0.74. August = 0.70 November = 0.76). The niche width was also calculated for low, medium and high intensity infections (Low = 0.71, Medium = 0.68. High = 0.76).

Table 5.1 Summary statistics for the distribution of *P. laevis* in the intestine of wild trout from Lough Feeagh for the total sample and for each month.

	April	May	August	November	Total
Count	95	566	357	170	1188
Mean ($\pm$ S.D.)	82.76(7.20)	79.76(12.32)	75.75(11.74)	73.33(11.82)	77.87(12.06)
Median	83.2	80	76.65	74.31	79.23
Inter quartile	4.5	12.74	11.23	14.06	11.59
Range					
Minimum	47.2	29.6	35.5	31.49	29.6
Maximum	98.8	100	99.18	98.94	100
Range	51.6	70.4	63.68	67.45	70.4
Skewness	-0.98	-1.15	-1.35	-0.56	-1.09
Kurtosis	5.40	2.58	2.67	1.41	2.33
Lower (25%)	80.6	74.68	72.075	66.95	73.51
Upper (75%)	85.1	87.42	83.3	81.01	85.1

Table 5.2 Summary statistics for the distribution of *P. laevis* in the intestine of wild trout from Lough Feeagh at low (1-5 worms), medium (6-9 worms) and high (10+ worms) infection intensities.

	Low	Medium	High
Count	256	137	795
Mean ($\pm$ S.D.)	79.06(9.25)	80.73(10.51)	77(12.98)
Median	78.5	80.2	79.06
Inter quartile	10.03	12.18	13.67
Range			
Minimum	43.47	31.49	29.6
Maximum	99.35	100	100
Range	55.88	68.51	70.4
Skewness	-0.18	-1.16	-1.09
Kurtosis	1.35	0.90	1.81
Lower (25%)	74.34	75.32	71.43
Upper (75%)	84.37	87.5	85.1

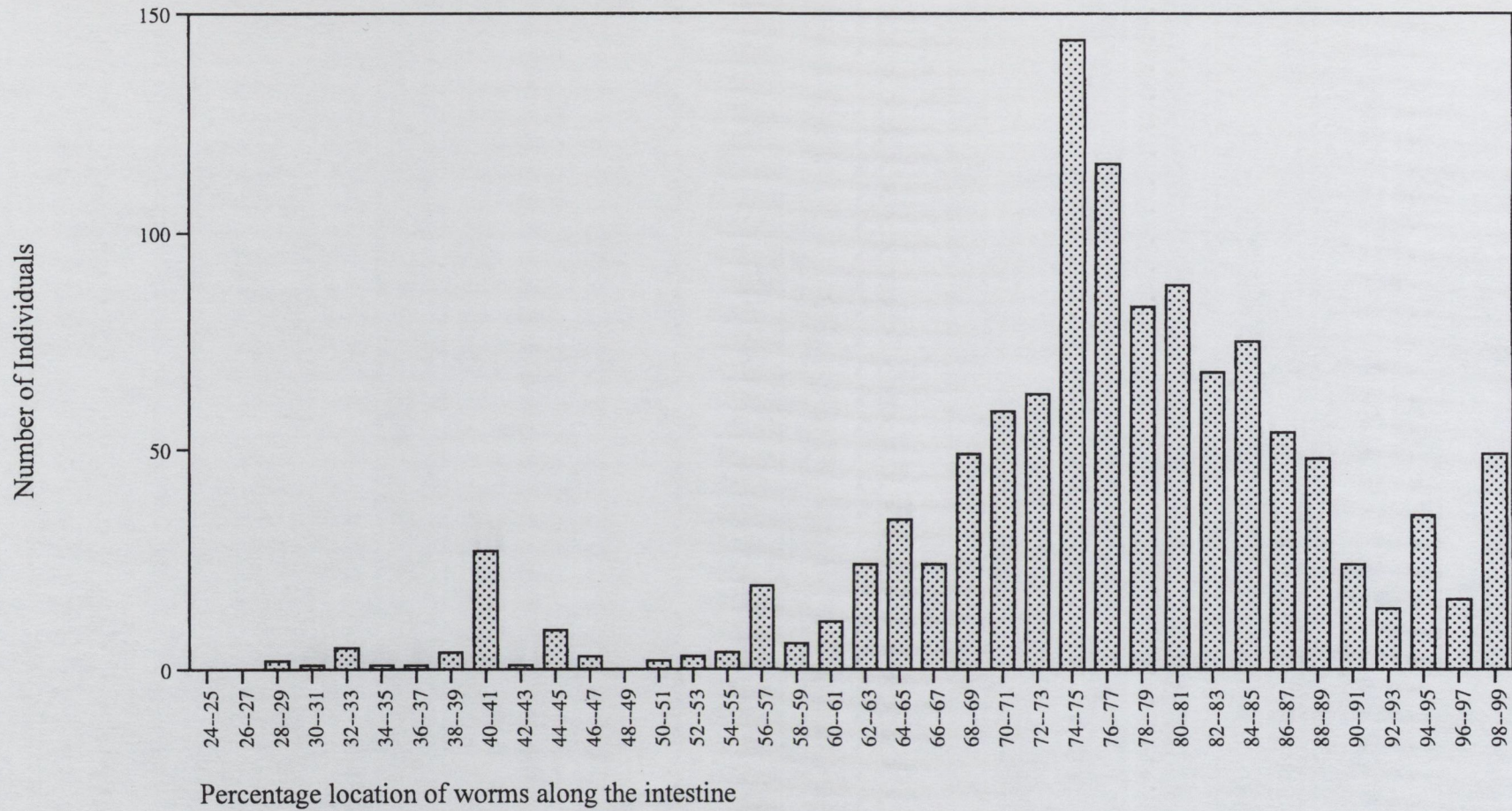


Fig 5.1 Fundamental niche of *P. laevis* along the intestine of wild trout from Lough Feeagh.

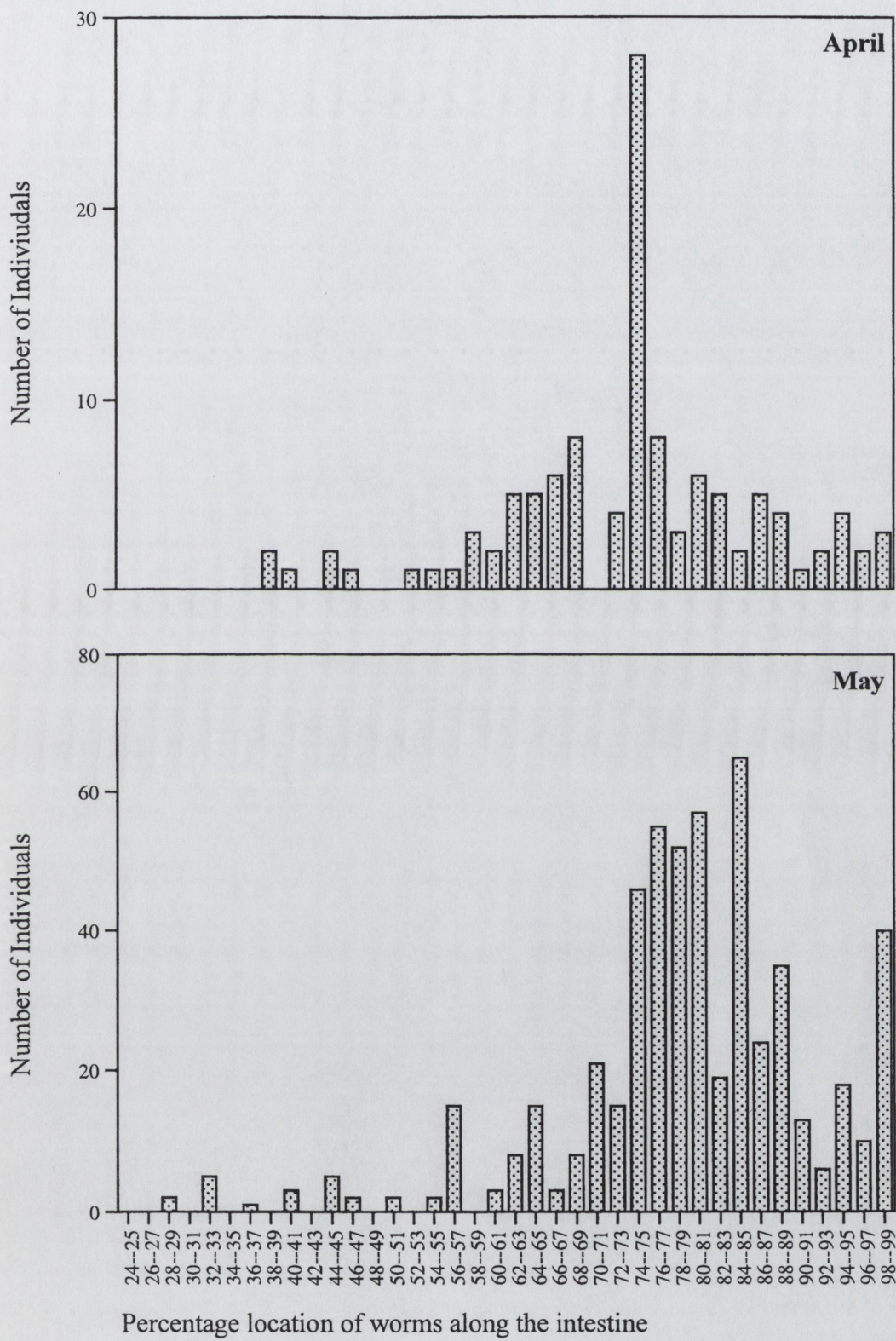


Fig 5.2 Niches for *P. laevis* along the intestine of wild trout in Lough Feeagh in April and May.

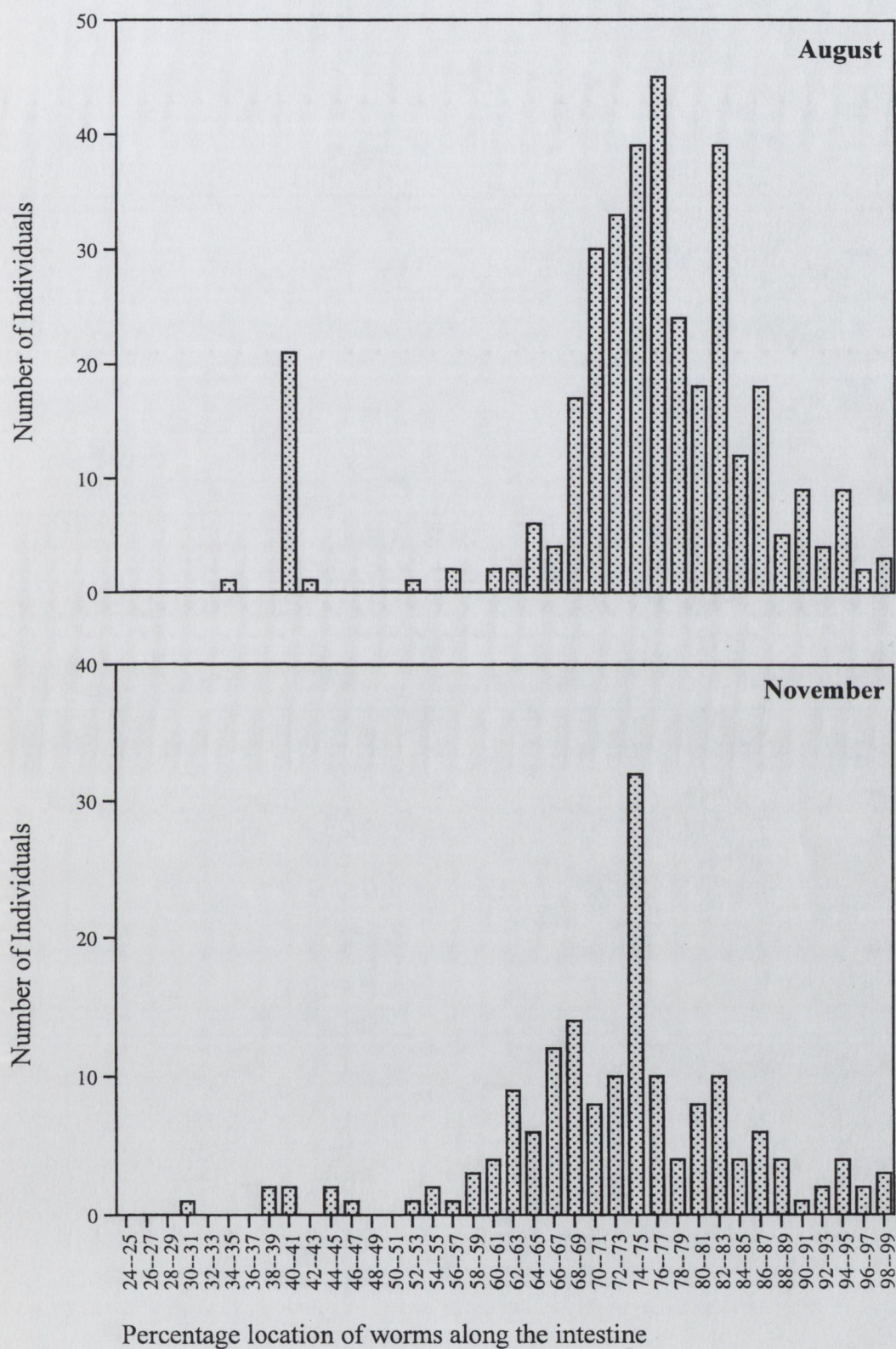


Fig 5.3 Niches for *P. laevis* along the intestine of wild trout in Lough Feeagh in August and November.

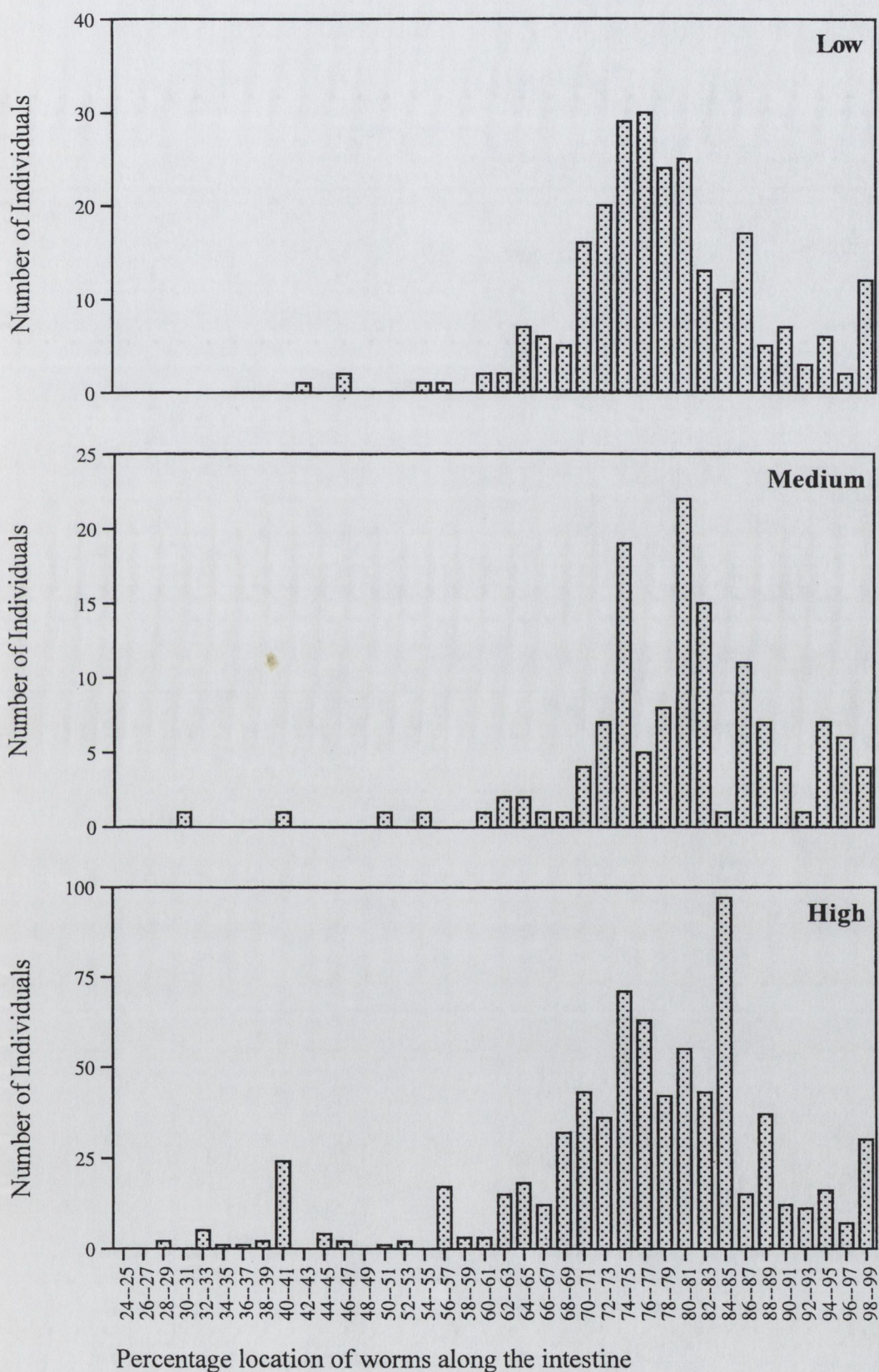


Fig 5.4 Niches of *P. laevis* in low intensity (1-5 worms), medium intensity (6-9 worms) and high intensity (10+ worms) infections along the intestine of wild trout from Lough Feeagh.

5.2.4 *P. laevis* in stocked trout

Figure 5.5 shows the fundamental niche of *P. laevis* for the total stocked trout sample. This was then divided and the niche of *P. laevis* was examined for each sample month (Fig 5.6) and finally the total sample of *P. laevis* was divided into low, medium and high intensity infections and the niche was examined at each intensity (Fig 5.7).

5.2.5 Total sample of *P. laevis* examined by month

62 worms were recovered from stocked trout in Lough Feeagh in May, 9 were recovered in August and 449 were recovered in November. A total of 520 *P. laevis* were recovered from the total stocked trout sample (Table 5.3; Fig 5.5). The mean percentage location of *P. laevis* in the intestine was highest in August and lowest in November. However, the mean location values recorded in May and November were comparable (Table 5.3).

Median values followed a similar pattern, values recorded in May and November were similar, but August still had the highest median value and November had the lowest. Median values were higher than mean values in May and November and lower than mean values in August (Table 5.3).

The maximum location of *P. laevis* along the intestine increased from May to November. Minimum values were more variable, they decreased from a peak in August to their lowest level in November. Correspondingly, the range of occurrence of *P. laevis* along the intestine was comparable for May and November but substantially lower in August.

Values for the lower 25% quartile were comparable for May and November and slightly higher in August. The same pattern occurred for the 75% quartile values, but the value recorded in August was substantially higher than the values recorded in May or November. Thus, the interquartile range was comparable for May and November and substantially higher in August (Table 5.3).

Skewness values were negative in May and November and positive in August. In all cases values were below one. Kurtosis values were positive and below one in May and November and negative and above one in August. This suggests that the distribution of *P. laevis* in May and November was reasonably peaked and approximated a normal distribution with no obvious asymmetric tails, whereas the distribution of *P. laevis* in August also approximated a normal distribution but was relatively flattened (Fig 5.6).

One-way analysis of variance (ANOVA) showed significant differences in the distribution of *P. laevis* along the intestine between months for the overall sample (F ratio = 2.3; df = 5,514; p = 0.045). Least squares difference post hoc tests showed which sample months had significantly different distributions from each other. Of the fifteen possible paired month combinations from the (six sample months), four pairs were significantly different from each other. Results are presented in Appendix 2, Table 2.

5.2.6 Total sample of *P. laevis* examined by intensity of infection

The total sample of *P. laevis* was split into low, medium and high intensity infections (Table 5.4; Fig 5.7). The same parameters were used to define low, medium and high intensity infections in stocked trout as were used for wild trout.

97 *P. laevis* were found in low intensity infections 124 *P. laevis* were found in medium intensity infections and 299 *P. laevis* were found in high intensity infections. The mean position of *P. laevis* along the intestine was very similar for low and medium intensity infections, but lower for high intensity infections (Table 5.3).

Median positions followed the same pattern. They were comparable for low and medium intensity infections and lower for high intensity infections. In all cases median values were higher than mean values (Table 5.4). Median values were within the range of median values recorded when the total sample was examined by month (Table 5.3).

Maximum values increased from low intensity to high intensity infections. The lowest minimum position was recorded for high intensity infections, and the highest minimum position along the intestine was recorded in medium intensity infections. Correspondingly, the range of occurrence of *P. laevis* was lowest in medium intensity infections and highest in high intensity infections (Table 5.4).

Values for the 25% and 75% quartiles increased from low to medium intensity infections and then decreased in high intensity infections (Table 5.4). Thus, the interquartile range was highest in medium intensity infections but lowest in high intensity infections. In all cases interquartile range values were comparable (Table 5.4).

Skewness values were negative and below one for low, medium and high intensity infections. Kurtosis values were positive for low and high intensity infections and negative for medium intensity infections. For low medium and high intensity infections the distribution of *P. laevis* along the intestine approximated a normal distribution. It was not overtly peaked or flattened and did not have any obvious asymmetric tails (Table 5.4; Fig 5.7).

One-way analysis of variance (ANOVA) showed significant differences in the distribution of *P. laevis* along the intestine between low, medium and high intensity infections (F ratio = 6.3; df = 2, 517; $p \leq 0.002$). Least squares difference post hoc tests showed significant differences in the distribution of *P. laevis* between high and low ($p \leq 0.005$) and between high and medium intensity infections ($p \leq 0.004$). The most anterior mean position was recorded in high intensity infections, and in medium and low intensity infections mean positions were comparable and more posterior.

The niche width was calculated for the total sample (0.80) and for each sample month (0.75 in May, 0.44 in August and 0.79 in November). Niche width values decreased from 0.75 in low intensity infections to 0.74 in medium intensity infections and then increased to 0.76 in high intensity infections. The niche widths recorded for low,

medium and high intensity infections were within the range of niche widths recorded for the sample months.

Table 5.3 Summary statistics for the distribution of *P. laevis* in the intestine of stocked trout from Lough Feeagh for the total sample and for each month.

	May	August	November	Total
Count	62	9	449	520
Mean ($\pm$ S.D.)	70.73(13.31)	81.27(14.74)	70.21(11.62)	70.46(11.96)
Median	72.9	78.13	71.06	68.14
Inter quartile	14.46	27.89	12.97	13.27
Range				
Minimum	37.26	62.65	37.14	37.14
Maximum	94.2	97.7	99.14	99.14
Range	56.94	35.05	62	62
Skewness	-0.61	0.02	-0.4	-0.38
Kurtosis	0.05	-1.77	0.6	0.51
Lower (25%)	64.93	67.57	64.08	64.15
Upper (75%)	79.39	95.46	77.05	77.41

Table 5.4 Summary statistics for the distribution of *P. laevis* in the intestine of stocked trout from Lough Feeagh at low (1-5 worms), medium (6-9 worms) and high (10+ worms) infection intensities.

	Low	Medium	High
Count	97	124	299
Mean ($\pm$ S.D.)	72.76(11.52)	72.49(12.19)	68.88(11.78)
Median	73.11	73.90	70.23
Inter quartile	13.27	13.83	12.38
Range			
Minimum	37.24	41.43	37.14
Maximum	97.7	98.26	99.14
Range	60.46	56.83	62
Skewness	-0.25	-0.52	-0.39
Kurtosis	0.33	-0.08	0.88
Lower (25%)	66.66	66.91	63.04
Upper (75%)	79.93	80.74	75.42

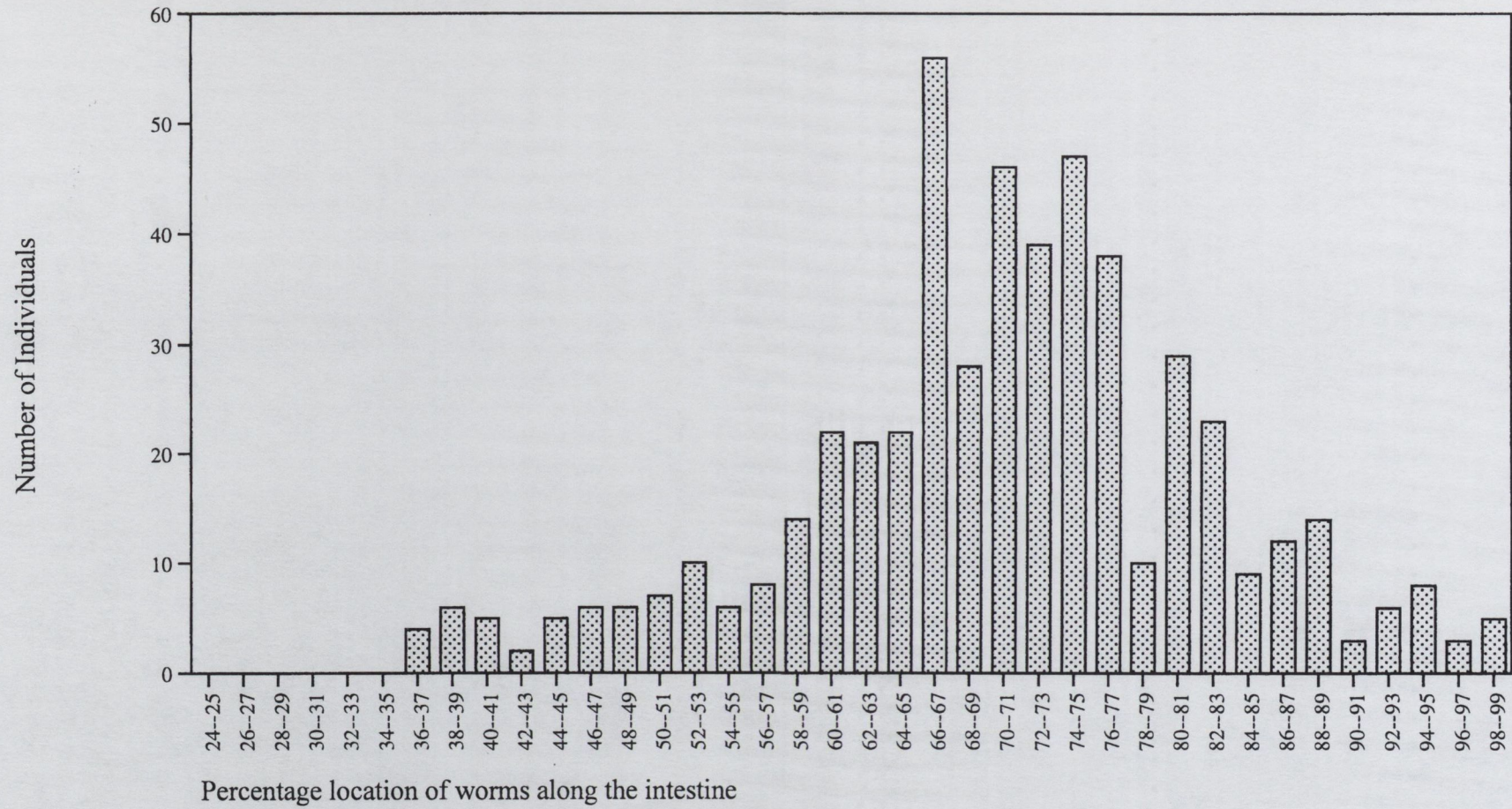


Fig 5.5 Fundamental niche of *P. laevis* along the intestine of stocked trout from Lough Feeagh.

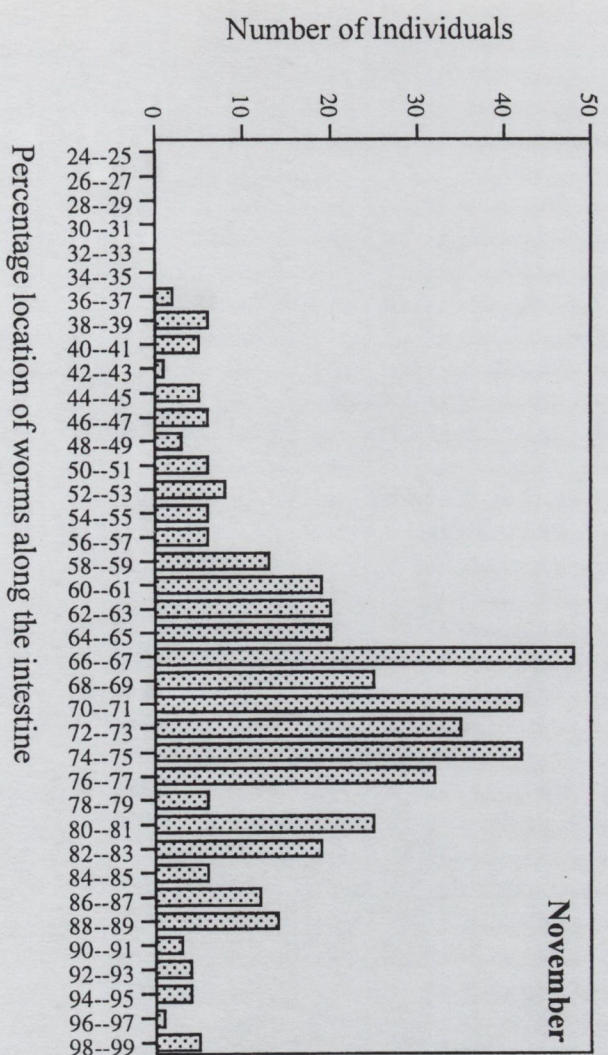
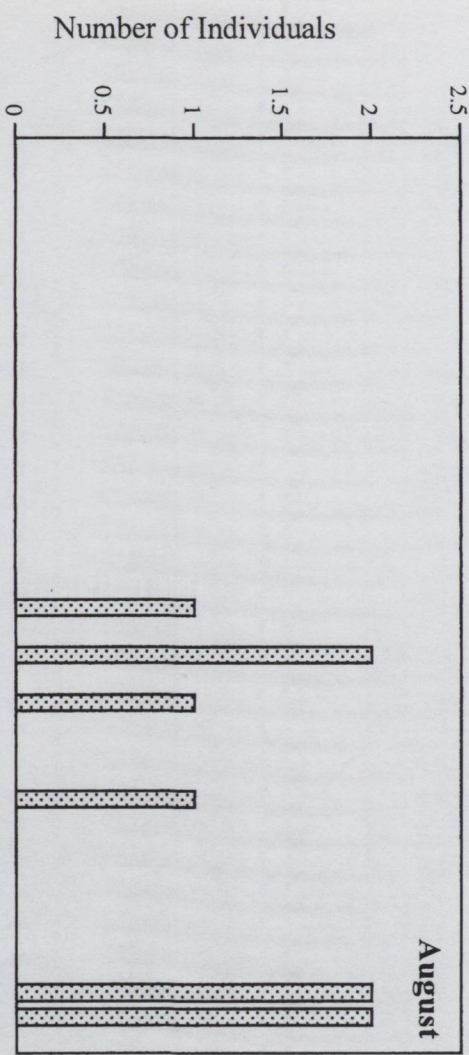
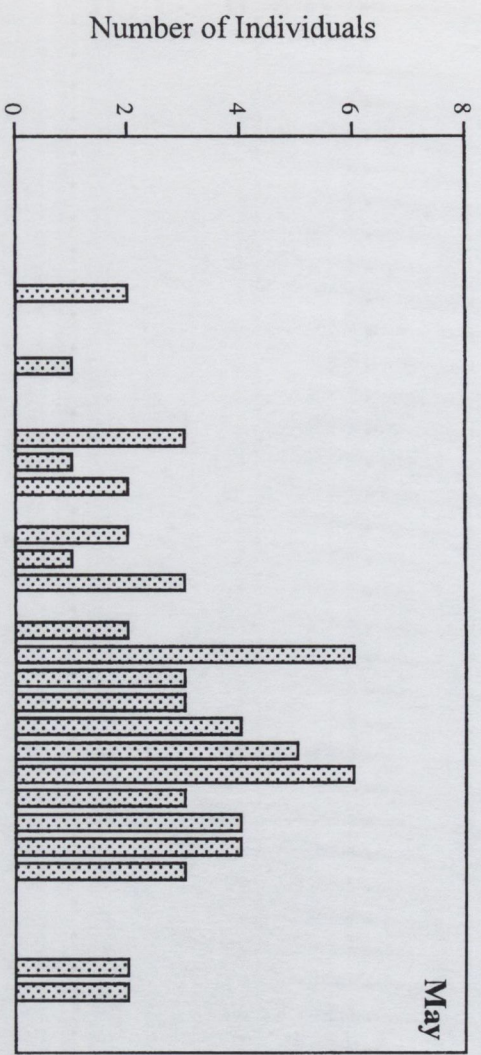


Fig 5.6 Niches for *P. laevis* along the intestine of tagged trout in Lough Feeagh in May, August and November.

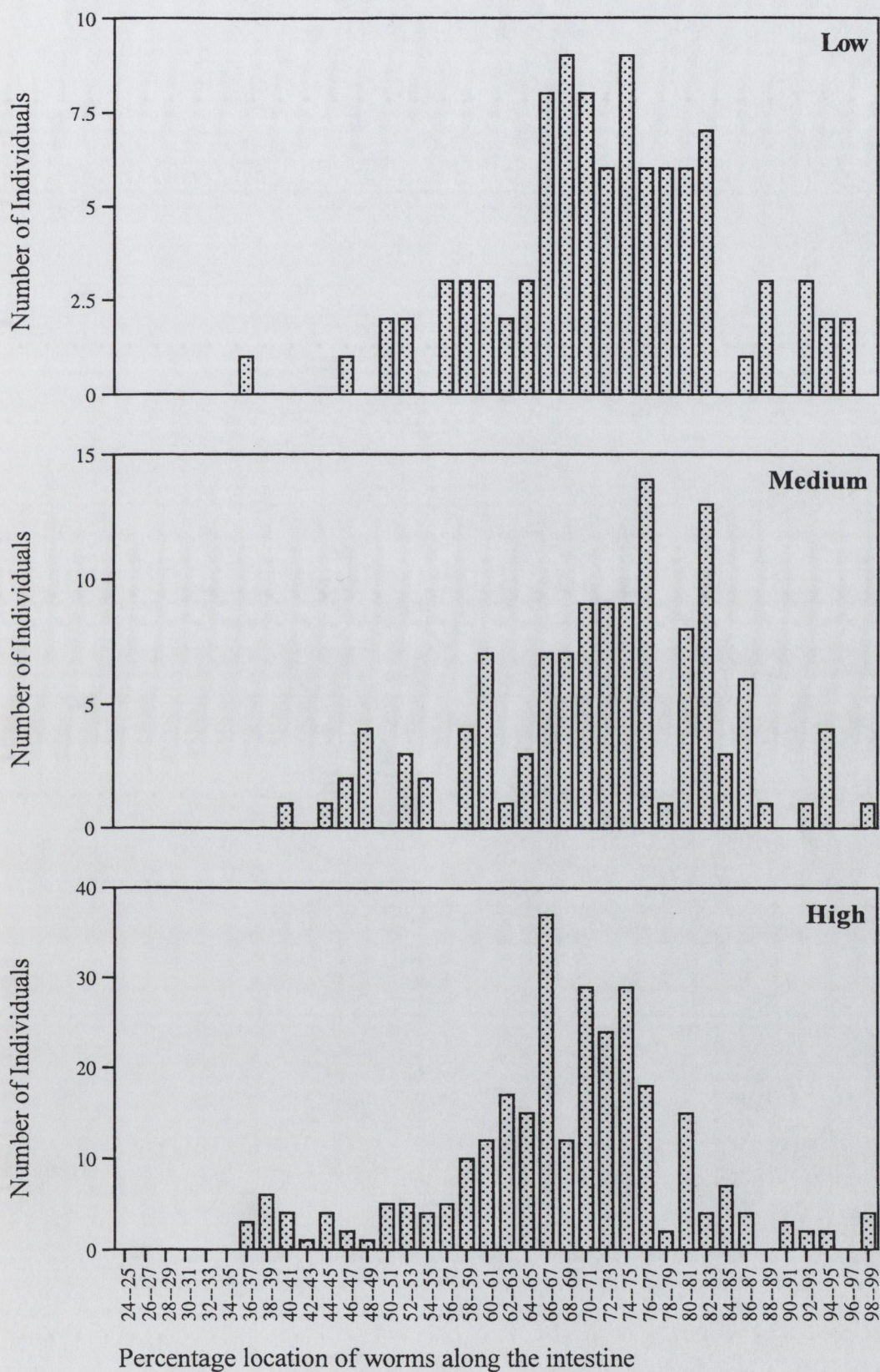


Fig 5.7 Niches of *P. laevis* in low intensity (1-5 worms), medium intensity (6-9 worms) and high intensity (10+ worms) infections along the intestine of stocked trout from Lough Feeagh.

5.3 Comparison of the niches of *P. laevis* in wild and stocked trout in Lough Feeagh

5.3.1 *P. laevis* in wild and stocked trout compared by month

In this section the niches of *P. laevis* in wild and stocked trout were compared by sample month and then by intensity of infection. A total of 1188 *P. laevis* were found in wild trout (Table 5.1) compared to 520 in stocked trout (Table 5.3). In wild trout approximately 47% of all worms were found in May, 30% in August and 14% in November, in contrast to this in stocked trout 12% of worms were found in May, 2% were found in August and 86% were found in November (Table 5.1; Table 5.3).

In wild trout the mean position of *P. laevis* decreased from a peak in April to the lowest value in November (Table 5.1). In stocked trout the mean position increased substantially from May to August and decreased again in November (Table 5.3). The mean position of *P. laevis* was lower for stocked trout in May and November and higher in August. The mean position of *P. laevis* for the total sample in wild trout was higher than the value recorded for the total sample of stocked trout (Table 5.1).

Median values followed the same pattern as mean values, in wild trout they decreased from April to November and in all cases median values were higher than mean values (Table 5.1). Median values for stocked trout also followed the same pattern as mean values. They increased from May to August and decreased in November. Median values were higher than mean values in May and August (Table 5.3).

Minimum values for *P. laevis* in wild trout fluctuated from 47.2% in April to 29.6% in May. Maximum values were much more consistent and ranged from 98.8% in April to 100% in May, thus most of the variation in the range of occurrence of *P. laevis* in wild trout was as a result of fluctuation in minimum values. The range of occurrence of *P. laevis* in wild trout was lowest in April, highest in May and comparable for August and November (Table 5.1). In stocked trout the minimum values for *P. laevis* were all higher than in wild trout and maximum values were all

lower than in wild trout. Minimum values increased from May to August and decreased in November, whereas maximum values increased from May to November. Correspondingly, the range of occurrence of *P. laevis* in stocked trout decreased from May to August and increased in November (Table 5.3). In all cases the range of occurrence of *P. laevis* recorded in stocked trout was considerably smaller than that recorded in wild trout.

25% quartile values for wild trout decreased from April to November, and 75% quartile values decreased from May to November (Table 5.1). Thus, the interquartile range for *P. laevis* in wild trout increased from April to a peak in November. In stocked trout 25% quartile values increased from May to August and decreased in November. 75% quartile values followed a similar pattern increasing from May to August and decreasing in November. Thus the interquartile range of *P. laevis* in stocked trout also increased from May to August and decreased in November (Table 5.3). 25% and 75% quartile values in May and November were lower for stocked trout. Only the 75% quartile value recorded in August was higher for stocked trout. Interquartile ranges were comparable between wild and stocked trout in May and November and for the total sample, but were substantially higher for stocked trout in August.

Skewness values for *P. laevis* in wild trout were all negative, and greater than one in May and August, suggesting negative asymmetric tails. Kurtosis values were all positive suggesting peaked distributions. In wild trout skewness values were negative and below one in May and November, and positive and below one in August, suggesting normal distributions. Kurtosis values were positive in May and November and negative in August, suggesting slightly peaked distributions in May and November and a flattened distribution in August.

One-way analysis of variance (ANOVA) was used to compare the distribution of *P. laevis* along the intestine between wild and stocked trout for each sample month and the total sample. Significant differences were found in the distribution of *P. laevis*

between wild and stocked trout for the total sample (F ratio = 137.2; df = 1,1706; $p \leq 0.0001$) and for each sample month, May (F ratio = 25.7; df = 1,626; $p \leq 0.0001$), August (F ratio = 1.9; df = 1.364; $p \leq 0.0001$) and November (F ratio = 8.8; df = 1,617; $p \leq 0.003$). The mean position recorded for *P. laevis* in wild trout was more posterior than that recorded for *P. laevis* in stocked trout in May, November and for the total sample. In August the mean position recorded for *P. laevis* in stocked trout was more posterior.

5.3.2 *P. laevis* in wild and stocked trout compared by intensity of infection

In this section the total sample of *P. laevis* in wild and stocked trout was compared between low, medium and high intensity infections. Of the total 1188 *P. laevis* found in wild trout, 256 were in low intensity infections, 137 were in medium intensity infections and 795 were in high intensity infections (Table 5.2). In stocked trout 97 worms were found in low intensity infections, 124 worms were found in medium intensity infections and 299 worms were found in high intensity infections (Table 5.4).

In wild trout the mean position decreased from a peak in medium intensity infections to the lowest value in high intensity infections (Table 5.2). In stocked trout the mean position was practically identical for low and medium intensity infections and it decreased in high intensity infections (Table 5.4). The mean position of *P. laevis* in low, medium and high intensity infections was more anterior in stocked trout.

Median position values for *P. laevis* in wild trout increased from low intensity infections to a peak in medium intensity infections and then decreased in high intensity infections. (Table 5.2). In stocked trout median values were nearly identical for low and medium intensity infections and decreased for high intensity infections. In all cases the median position values recorded for *P. laevis* in stocked trout were lower than the median position values recorded in *P. laevis* in wild trout.

The range of occurrence of *P. laevis* in wild trout increased from low to high intensity infections (Table 5.2). In stocked trout the range of occurrence of *P. laevis* decreased from low to medium intensity infections and increased in high intensity infections (Table 5.4). The range of occurrence of *P. laevis* was substantially higher in medium and high intensity infections in wild trout. Stocked trout had the highest range of occurrence in low intensity infections.

The interquartile range for *P. laevis* in wild trout increased from low to high intensity infections (Table 5.2). The interquartile range for *P. laevis* in stocked trout increased from low intensity infections to a peak in medium intensity infections and then decreased to its lowest value in high intensity infections (Table 5.4). In all cases 25% quartile and 75% quartile values were higher in wild trout, but the interquartile range values were comparable between wild and stocked trout for medium and high intensity infections.

Skewness values for *P. laevis* in wild trout in low, medium and high intensity infections were all negative, and for medium and high intensity infections they were above one. Kurtosis values were all positive, suggesting that *P. laevis* had a peaked distribution which approximated normal in low intensity infections and a peaked distribution with negative asymmetric tails in medium and high intensity infections (Table 5.2). In stocked trout skewness values were all negative and below one, and kurtosis values were positive for low and high intensity infections and negative for medium intensity infections. This suggests that *P. laevis* had peaked distributions which approximated normal in low and high intensity infections and a flattened distribution which approximated normal in medium intensity infections (Table 5.4).

The niche width of *P. laevis* for the total sample in wild trout (0.71) was considerably smaller than the corresponding value in stocked trout (0.80). However niche widths were comparable between wild and stocked trout for May and November, but the niche width value recorded for stocked trout in August, 0.44 was substantially smaller than the value recorded for wild trout in August, 0.70. Niche width values for wild

and stocked trout were comparable for low and high intensity infections but for medium intensity infections the niche width value recorded in wild trout, 0.68 was smaller than the corresponding value in stocked trout 0.74.

Two-way analysis of variance (ANOVA) was used to examine the distribution of *P. laevis* in the intestine between wild and stocked trout and for low, medium and high intensity infections. Significant differences in the distribution of *P. laevis* were shown to exist between wild and stocked trout (F ratio = 108.5; df = 1,1703; $p \leq 0.0001$). Significant differences also existed in the distribution of *P. laevis* between low, medium and high intensity infections (F ratio = 14; df = 2,1703; $p \leq 0.0001$), however the interaction between fish status (wild or stocked trout) and infection intensity (low, medium or high) was not significant. In all cases the distribution of *P. laevis* was more posterior in wild trout and more anterior in high intensity infections.

5.4 Examination of the niche of *A. clavula* in the intestine of wild and stocked trout in Lough Feeagh

The niche occupied by the acanthocephalan *A. clavula* in wild and stocked trout in Lough Feeagh was examined in detail. Its distribution along the intestine was calculated for the overall total sample (both years combined) and also for each sample month. In all cases a set of statistics summarising the distribution of *A. clavula* along the intestine have been provided. Finally the distribution of *A. clavula* along the intestine was compared between wild and stocked trout

5.4.1 *A. clavula* in wild trout

A. clavula along the intestine of wild trout from Lough Feeagh were treated in the same manner as *P. laevis*. The distribution of the total sample of *A. clavula* from all wild fish in Lough Feeagh was first examined (Fig 5.8). The total sample was then examined by month, and at low, medium and high intensity infections (Figs 5.9-5.11).

5.4.2 Total sample of *A. clavula* examined by month

730 worms were found in the wild trout sample in Lough Feeagh (Fig 5.8), 58 in April, 292 in May, 233 in August and 147 in November. The mean position of *A. clavula* along the intestine decreased substantially from April to November. Median values followed exactly the same pattern (Table 5.5; Figs 5.9-5.10).

Maximum position values decreased from 100% in April to 94.28% in November. The lowest minimum value, 29.15%, was recorded in August. The range of occurrence of *A. clavula* increased from its smallest value in April to a peak in August, and then decreased again in November (Table 5.5; Figs 5.9-5.10).

25% and 75% quartile values decreased substantially from April to November. The interquartile range increased slightly from April to May, but then declined substantially in August and November (Table 5.5).

April had a negative skewness value suggesting a negative asymmetric tail (Fig 5.9). May and August had positive skewness values below one which suggested that they had distributions which approximated a normal distribution. November had a positive skewness value above one, which suggested a positive asymmetric tail. April, May and August had negative kurtosis values suggesting relatively flat distributions. In contrast November had a positive kurtosis value which suggested that the distribution of *A. clavula* was relatively peaked (Table 5.5; Fig 5.10).

One-way analysis of variance (ANOVA) was used to compare the distribution of *A. clavula* along the intestine for each sample month. A significant difference was shown to exist (F ratio = 47.8; df = 6,723; $p \leq 0.0001$). Least squares difference post hoc tests showed which of the sample months had significantly difference distributions from each other. Of the twenty-one possible combinations of sample months (from the seven months in the total sample), fourteen were significantly different from each other (See Appendix 2, Table 3).

5.4.3 Total sample of *A. clavula* examined by intensity of infection

The total sample of *A. clavula* was also examined for low, medium and high intensity infections. For *A. clavula* the same infection parameters were used in Lough Feeagh, as were used in Clogher Lake. An infection was of low intensity when one to fifteen worms occurred in a fish, of medium intensity when sixteen to seventy-five worms occurred in a fish, of high intensity when seventy-six worms or more occurred in a fish. Similar to the situation for *P. laevis*, the ranges for low, medium and high intensity infections of *A. clavula* were established by examining the raw data and constructing frequency histograms. Different, higher values were used for low medium and high intensity infections of *A. clavula* because in the majority of cases the infection levels for *A. clavula* in Lough Feeagh were significantly higher than for *P. laevis*. They were more comparable to the levels recorded in Clogher Lake.

For the total sample 205 worms were found in low intensity infections, 324 in medium intensity infections and 201 in high intensity infections. The mean location

of *A. clavula* decreased from low to high intensity infections (Table 5.6). The mean locations of *A. clavula* recorded in low, medium and high intensity infections were within the range of values recorded for the total sample. The lowest median value was recorded in medium intensity infections. The median values for low and high intensity infections were comparable (Table 5.6). All median values were within the range of values recorded for the total sample (Table 5.5). Maximum values decreased slightly from low to high intensity infections and minimum values were comparable between low, medium and high intensity infections. Thus, the range of occurrence of *A. clavula* was comparable for low, medium and high intensity infections (Table 5.6; Fig 5.11).

25% value quartile decreased from low to medium intensity infections and were comparable between medium and high intensity infections. 75% quartile values were comparable between low and medium intensity infections, but substantially lower for high intensity infections. Correspondingly, the interquartile ranges recorded for low and medium intensity infections were comparable and the range for high intensity infections was considerably smaller.

All three groups had positive skewness values. Only the high intensity infection had a skewness value above one (Fig 5.11). Kurtosis values were negative for low and medium intensity infections and positive for high intensity infections. This would suggest that low and medium intensity infections had flatter distributions, which approximated a normal and high intensity infections had a more peaked distribution with a positive asymmetric tail.

One-way analysis of variance (ANOVA) showed significant differences in the distribution of *A. clavula* between low, medium and high intensity infections for the total sample (F ratio = 22.4; df = 2,728; $p \leq 0.0001$). Least squares difference post hoc tests showed significant differences between medium and low ($p \leq 0.005$), high and low ($p \leq 0.0001$) and high and medium ($p \leq 0.0001$) intensity infections. The

mean position of *A. clavula* became more anterior from low to high intensity infections.

The niche width of *A. clavula* for the total sample was 0.86. Niche widths for the four sample months increased from, 0.70 in April, to a peak of 0.76 in May and August, and then decreased to their lowest value of 0.59 in November. Niche widths decreased from a peak of 0.86 in low intensity infections, to 0.82 in medium intensity infections and to their lowest value of 0.61 in high intensity infections.

Table 5.5 Summary statistics for the distribution of *A. clavula* in the intestine of wild trout from Lough Feeagh for the total sample and for each month.

	April	May	August	November	Total
Count	58	292	233	147	730
Mean ($\pm$ S.D.)	76.57(14.27)	67.49(16.01)	53.66(16.34)	47.11(12.61)	59.69(18.04)
Median	76.35	62.98	51.85	42.34	54.57
Inter quartile	24.4	25.19	19.1	6.82	29.35
Range					
Minimum	47.3	37.85	29.15	32.47	29.15
Maximum	100	99.39	98.1	94.28	100
Range	52.7	61.54	68.95	61.81	70.85
Skewness	-0.52	0.56	0.54	1.82	0.48
Kurtosis	-0.63	-0.83	-0.03	2.84	-0.61
Lower (25%)	63.4	53.21	45	41.3	45.65
Upper (75%)	87.8	78.4	64.1	48.12	75

Table 5.6 Summary statistics for the distribution of *A. clavula* in the intestine of wild trout from Lough Feeagh at low (1-15 worms), medium (16-75 worms) and high (76+ worms) infection intensities.

	Low	Medium	High
Count	203	324	201
Mean ($\pm$ S.D.)	64.98(19.23)	60.54(19.31)	53.2(11.64)
Median	64.55	57.14	65.15
Inter quartile	28.91	31.69	9.35
Range			
Minimum	31.25	29.15	29.78
Maximum	100	99.35	99.03
Range	68.75	70.2	69.25
Skewness	0.08	0.28	1.19
Kurtosis	-0.96	-0.81	1.08
Lower (25%)	50.4	45	45.65
Upper (75%)	79.3	76.69	55

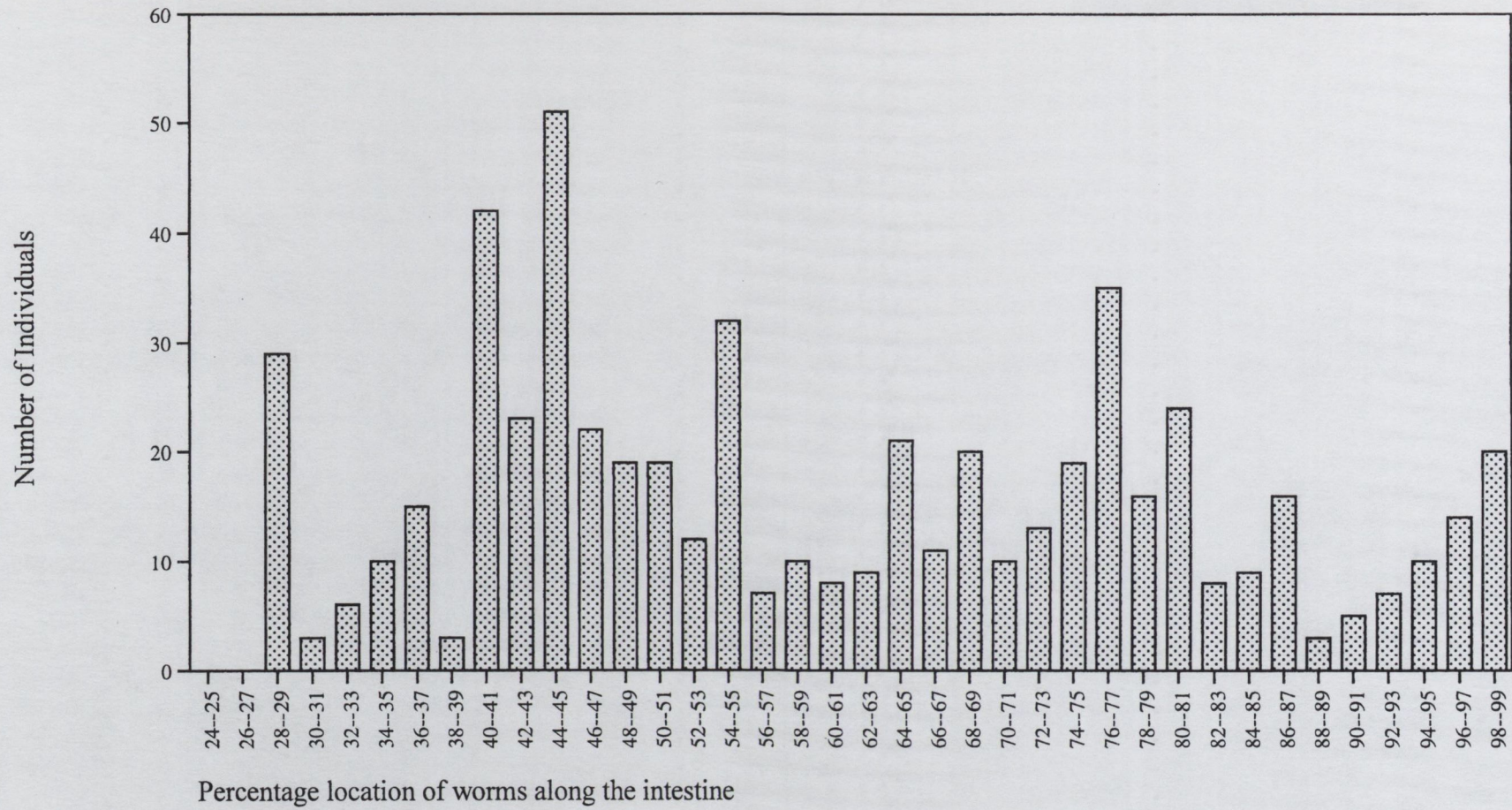


Fig 5.8 Fundamental niche of *A. clavula* along the intestine of wild trout from Lough Feeagh.

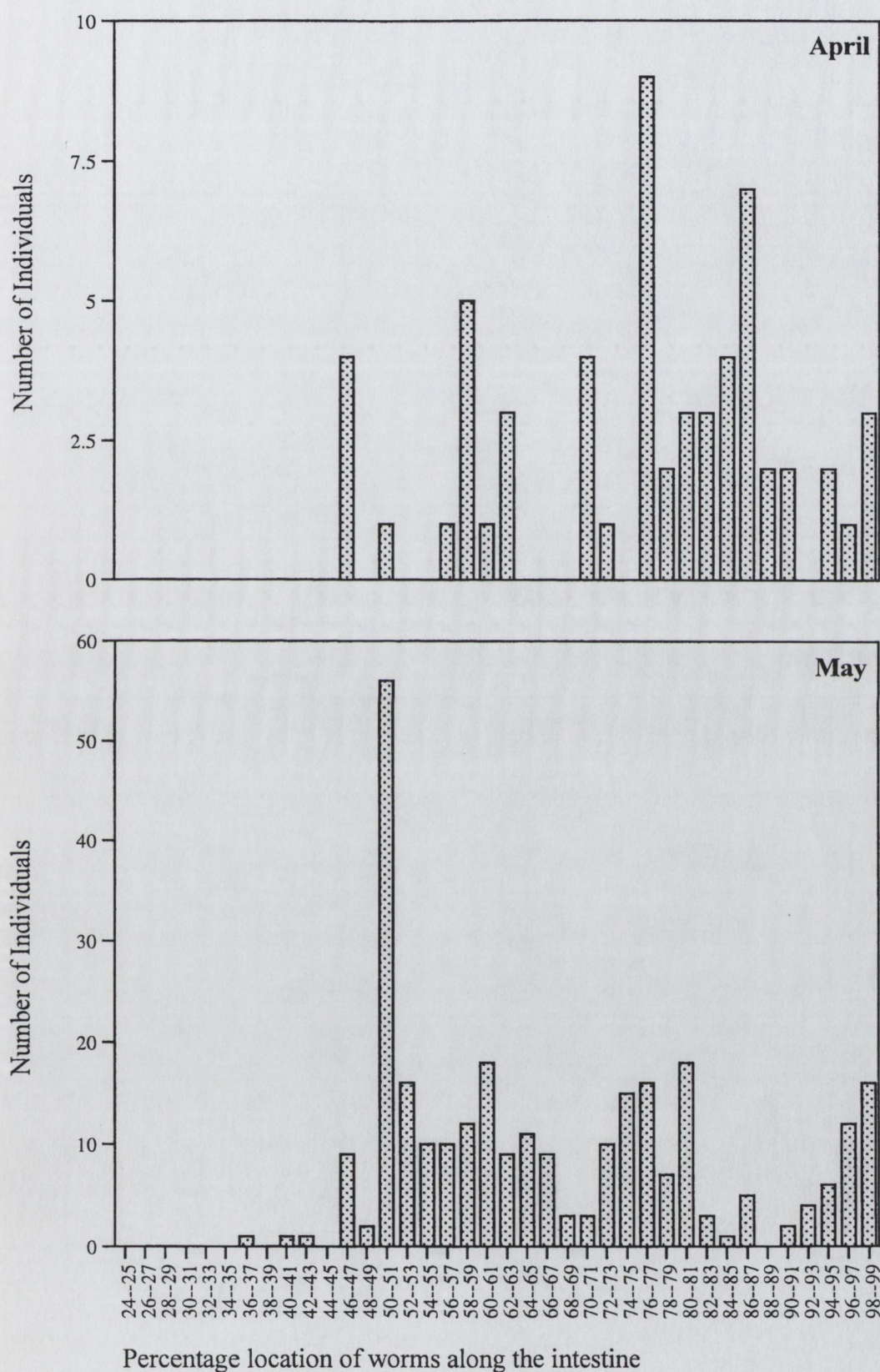


Fig 5.9 Niches for *A. clavula* along the intestine of wild trout in Lough Feeagh in April and May.

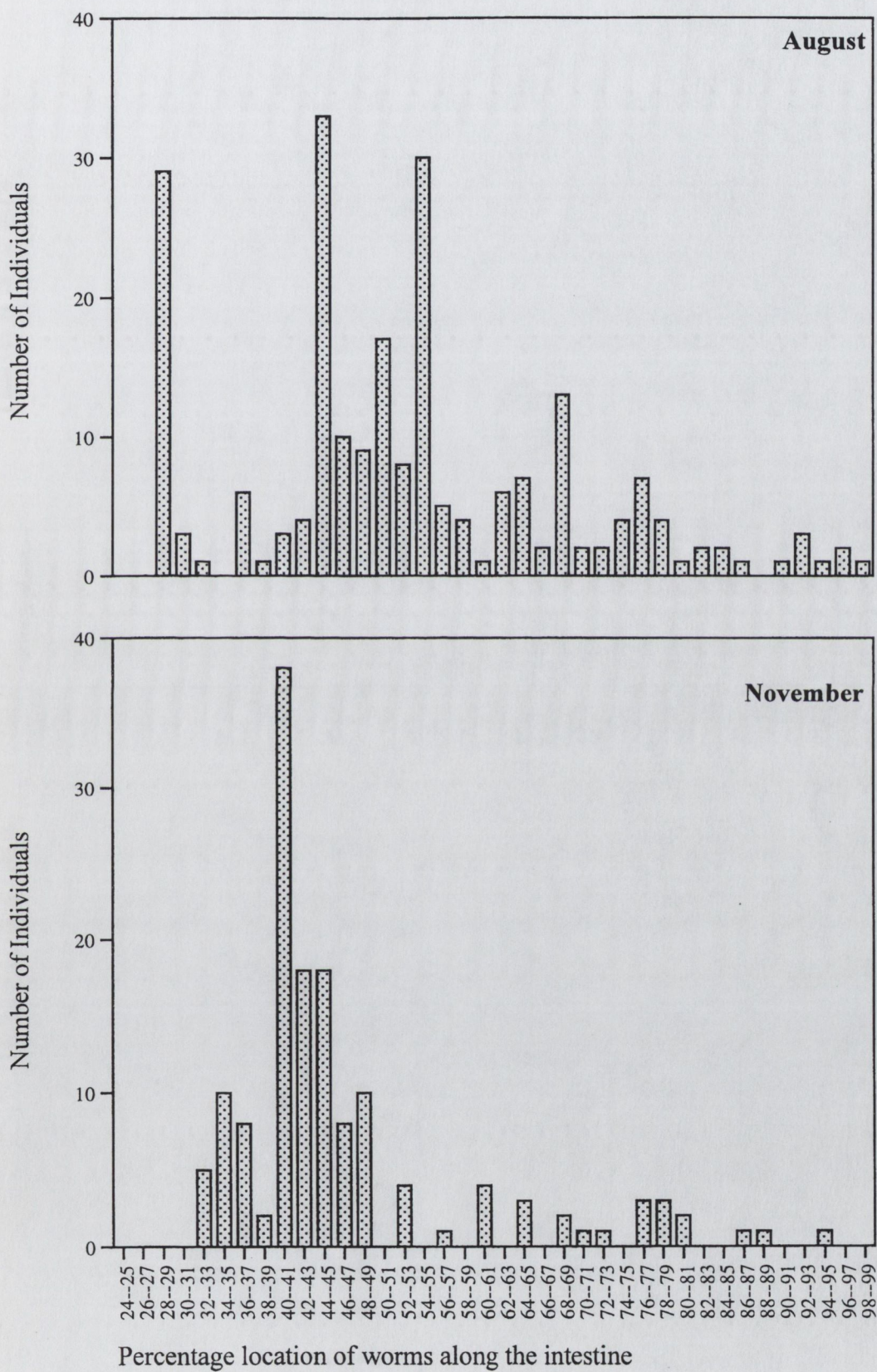


Fig 5.10 Niches for *A. clavula* along the intestine of wild trout in Lough Feeagh in August and November.

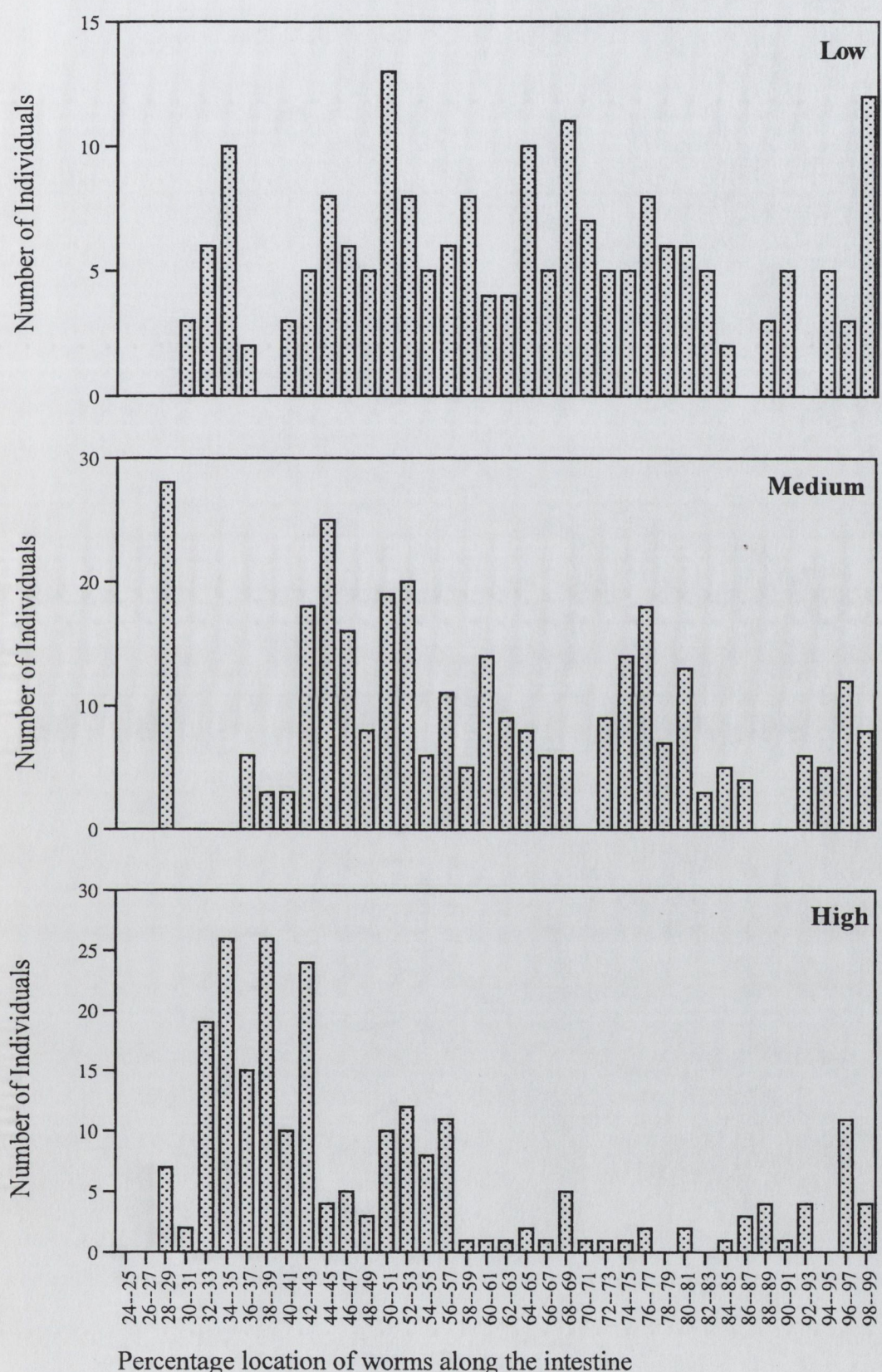


Fig 5.11 Niches of *A. clavula* in low intensity (1-15 worms), medium intensity (16-75 worms) and high intensity (76+ worms) infections along the intestine of wild trout from Lough Feeagh.

5.4.4 *A. clavula* in stocked trout

The distribution of *A. clavula* along the intestine of stocked trout in Lough Feeagh was examined in the same manner as *P. laevis*. The distribution of *A. clavula* in all stocked fish in Lough Feeagh was examined for the total sample (Fig 5.12), for each sample month (Table 5.7; Fig 5.13) and in low, medium and high intensity infections (Table 5.8; Fig 5.14).

5.4.5 Total sample of *A. clavula* examined by month

443 worms were found in the total sample of *A. clavula* in stocked trout, 137 were found in May, 188 in August and 118 in November. The mean position of *A. clavula* along the intestine was highest in May and lowest in August, and it increased again in November. August had the lowest median value, November had the highest and May had an intermediate mean value. In all months median values were lower than mean values (Table 5.7).

Minimum values decreased May to November and maximum values decreased from May to August and then increased in November. The relative consistency in maximum and minimum values was reflected in the range of occurrence of *A. clavula*. It ranged from 60.47% in August and 62.87% in November.

Values for the 25% and 75% quartiles were more variable. In both cases values for May and November were comparable but values for August were substantially lower. Although August had lower quartile values it had the largest interquartile range. The interquartile ranges for May and November were comparable (Table 5.7). Skewness and kurtosis values for all months were positive and below one suggesting that the distributions of *A. clavula* in the intestine of stocked trout in each sample month approximated normal distributions (Fig 5.13).

One-way analysis of variance (ANOVA) showed significant differences in the distribution of *A. clavula* between each sample month for the total sample (F ratio = 16.7; df = 5, 437; $p \leq 0.0001$). Least squares difference post hoc tests showed which

of the sample months had significantly different distributions from each other. Of the fifteen possible paired month combinations (from the six sample months), eight pairs were shown to significantly different from each other. Results are present in Appendix 2, Table 4.

5.4.5 Total sample of *A. clavula* examined by intensity of infection

The total sample of *A. clavula* was examined for low, medium and high intensity infections (Table 5.8; Fig 5.14). The same parameters were used to define low, medium and high intensity infections of *A. clavula* for stocked trout as were used for *A. clavula* in wild trout.

126 worms occurred in low intensity infections, 157 occurred in medium intensity infections and 160 occurred in high intensity infections. The mean position of *A. clavula* decreased from low to high intensity infections (Table 5.8). The mean position recorded in low intensity infections was higher than the mean position recorded for any sample month, and the mean position recorded for high intensity infections was lower than the mean position recorded for any sample month.

Median values followed the exact same pattern as mean values, decreasing from low to high intensity infections. In all cases median values were lower than mean values, they were also within the range of median values recorded for the total sample (Table 5.8).

Minimum values were very consistent and only varied by 0.75%. Maximum values were also relatively consistent and varied by about 4% from medium to high intensity infections. Thus the range of occurrence of *A. clavula* in the intestine of stocked trout was comparable between low, medium and high intensity infections.

Values for both the 25% and 75% quartile values decreased from low to high intensity infections to high intensity infections (Table 5.8). However, the interquartile range

was comparable between medium and high intensity and higher for low intensity infections.

Skewness values for low, medium and high intensity infections were positive. Medium and high intensity infections had skewness values above one. The kurtosis value was negative and below one for low intensity infections, positive and above one for medium intensity infections and positive and below one for high intensity infections. This suggests that the distribution of *A. clavula* was flattened but approximated a normal distribution in low intensity infections, peaked with a positive asymmetric tail in medium and high intensity infections (Fig 5.14).

One-way analysis of variance (ANOVA) showed significant differences in the distribution of *A. clavula* between low, medium and high intensity infections (F ratio = 16.2; df = 2, 428; $p \leq 0.0001$). Least squares difference post hoc tests showed a significant difference in the distribution of *A. clavula* between medium and low ($p = 0.018$), high and low ($p \leq 0.0001$) and high and medium intensity infections ($p \leq 0.0002$). Similar to the situation for *A. clavula* in wild trout, the mean position became more anterior from low to high intensity infections.

Niche width values were 0.75 in May, 0.65 in August and 0.71 in November. The niche width for the total sample was 0.79. Niche width values declined steadily from a peak of 0.80 in low intensity infections to 0.54 in high intensity infections. The niche width for medium intensity infections was 0.72. The niche width recorded for low intensity infections was larger than the value recorded in any sample month or the total sample.

Table 5.7 Summary statistics for the distribution of *A. clavula* in the intestine of stocked trout from Lough Feeagh for the total sample and for each month.

	May	August	November	Total
Count	137	188	118	443
Mean ($\pm$ S.D.)	54.56(13.75)	47.91(13.50)	53.8(14.71)	48.54(14.22)
Median	50	46.69	53.59	49.09
Inter quartile	16.34	19.26	18.34	18.93
Range				
Minimum	36.36	33.13	32.55	32.55
Maximum	97	93.6	95.42	97
Range	60.64	60.47	62.87	64.45
Skewness	0.94	0.95	0.86	0.88
Kurtosis	0.16	0.64	0.13	0.34
Lower (25%)	45	34.88	43.1	39.95
Upper (75%)	61.34	54.14	61.44	58.88

Table 5.8 Summary statistics for the distribution of *A. clavula* in the intestine of stocked trout from Lough Feeagh at low (1-15 worms), medium (16-75 worms) and high (76+ worms) infection intensities.

	Low	Medium	High
Count	126	157	160
Mean ($\pm$ S.D.)	55.87(14.68)	51.99(13.85)	46.49(12.81)
Median	53.36	50	46.08
Inter quartile	22.19	17.44	18.71
Range			
Minimum	32.55	33.3	33.13
Maximum	93.88	97	93.08
Range	61.33	63.7	59.95
Skewness	0.65	1.17	1.01
Kurtosis	-0.42	1.02	0.91
Lower (25%)	43.87	41.41	33.13
Upper (75%)	66.06	58.85	51.84

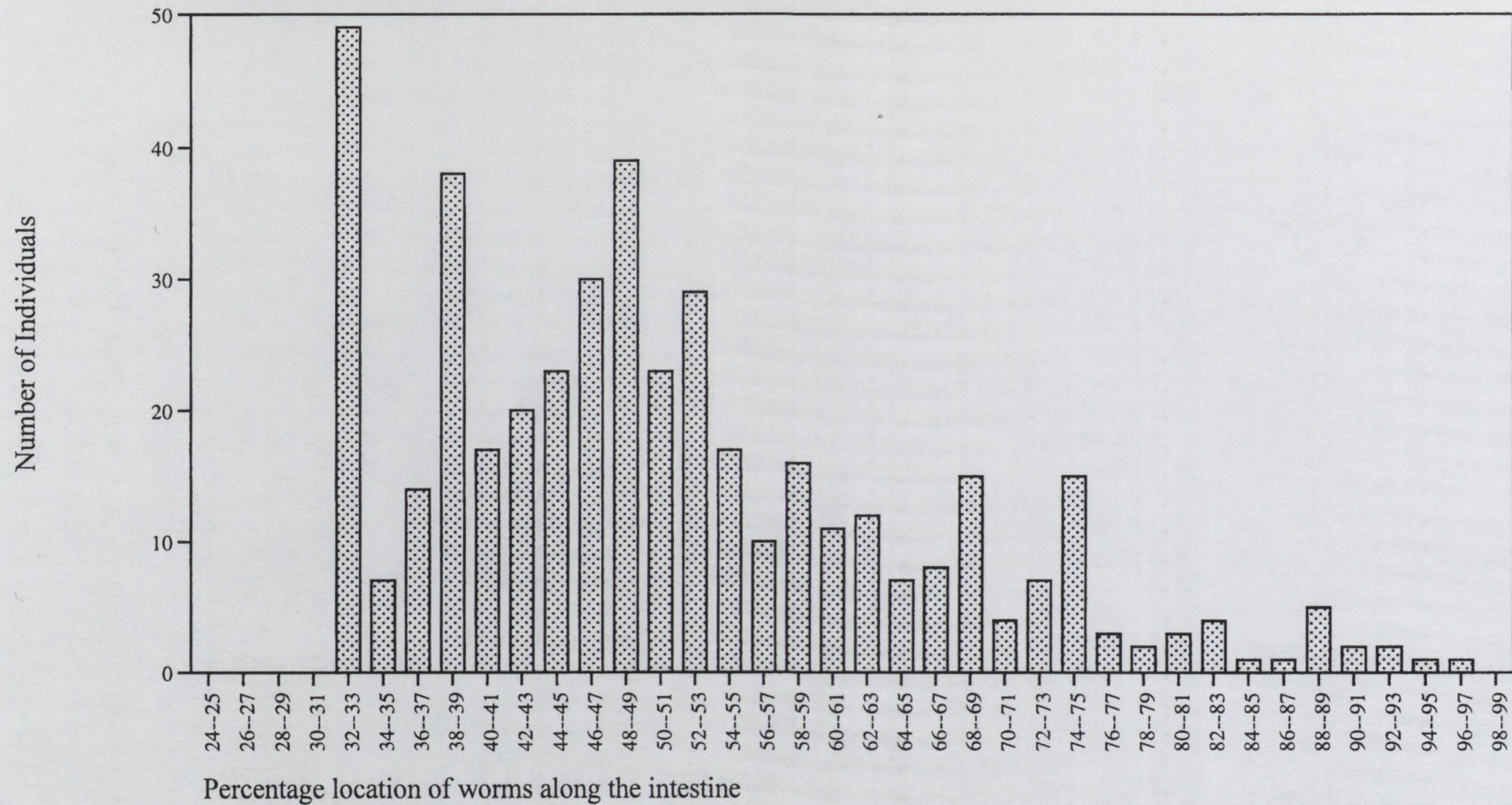


Fig 5.12 Fundamental niche of *A. clavula* along the intestine of stocked trout from Lough Feeagh.

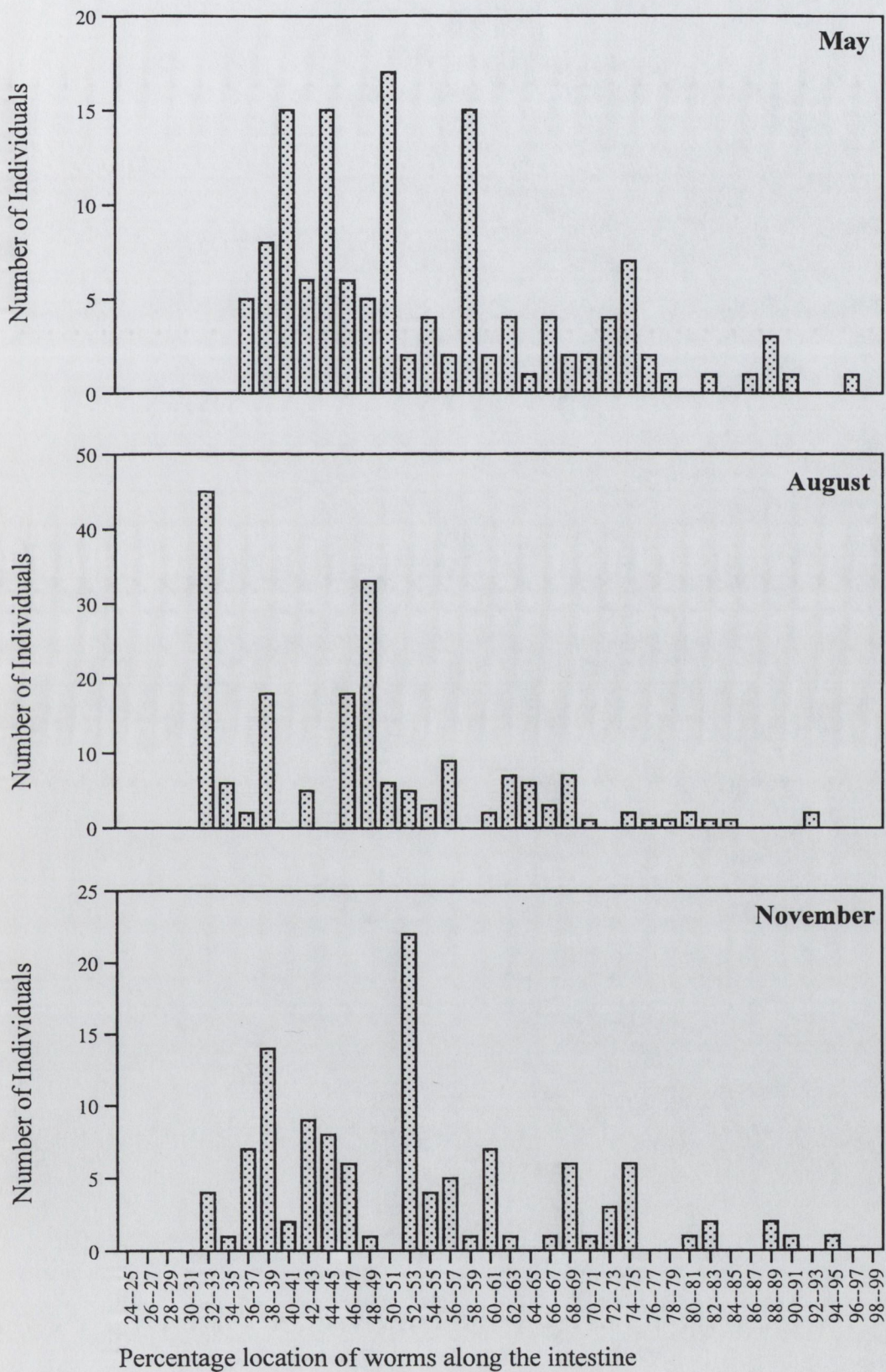


Fig 5.13 Niches for *A. clavula* along the intestine of stocked trout in Lough Feeagh in May, August and November.

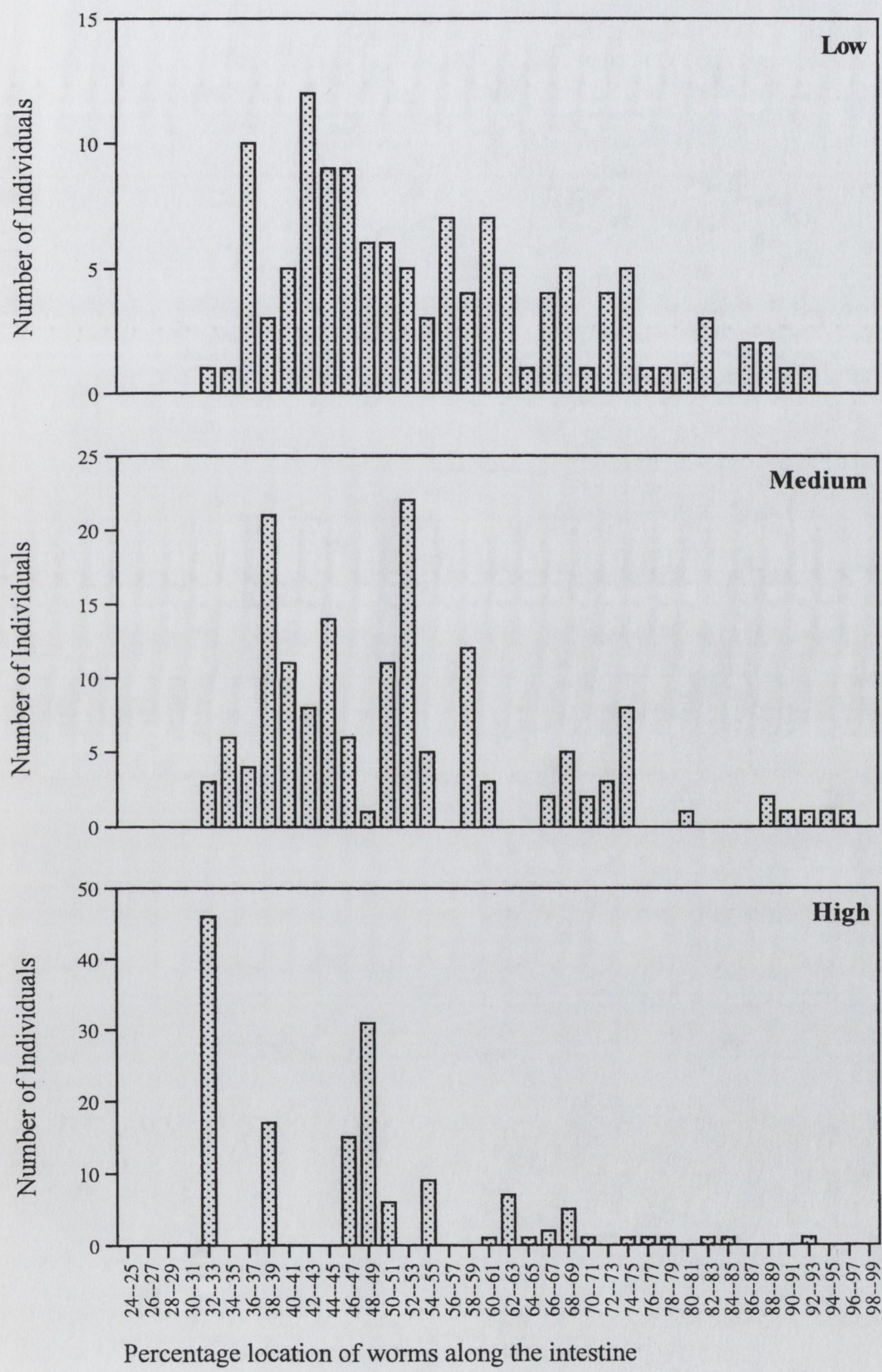


Fig 5.14 Niches of *A. clavula* in low intensity (1-15 worms), medium intensity (16-75 worms) and high intensity (76+ worms) infections along the intestine of stocked trout from Lough Feeagh.

5.5 Comparison of the niche of *A. clavula* in wild and stocked trout in Lough Feeagh

5.5.1 *A. clavula* in wild and stocked trout compared by month

In this section the niches of *A. clavula* in wild and stocked trout are compared by sample month and then by intensity of infection. A total of 730 *A. clavula* were found in wild trout, 58 were found in April, 292 were found in May, 233 in August and 147 were found in November (Table 5.5). In stocked trout 443 *A. clavula* were found 137 in May, 188 in August and 118 in November (Table 5.7).

The mean position of *A. clavula* in wild trout decreased from April to November (Table 5.5). In stocked trout the mean location of *A. clavula* decreased from May to August and increased again in November (Table 5.7). The mean position of *A. clavula* for the total sample and for May and August samples was substantially lower in stocked trout than in wild trout, however the mean position of *A. clavula* for the November sample was higher in stocked trout.

In wild trout median values followed the same pattern as mean values decreasing from April to November (Table 5.5). In stocked trout median values decreased from May to August and increased in November (Table 5.7). With the exception of the November sample, the median values for May, August and the total sample in stocked trout were considerably lower than the corresponding values in wild trout

Minimum values for *A. clavula* in stocked trout decreased from April to August and increased slightly in November and maximum values decreased from April to in November. Correspondingly the range of occurrence of *A. clavula* in wild trout increased from April to a peak in August and decreased in November (Table 5.5). In stocked trout minimum values for *A. clavula* decreased from May to November and maximum values decreased from May to August and in November. Thus the range of occurrence of *A. clavula* in stocked trout varied minimally from May to August and increased in November (Table 5.7). The range of occurrence of *A. clavula* in wild and

stocked trout was comparable for May and November, but was considerably higher for wild trout in August. The range of occurrence of *A. clavula* for the total sample was also higher for wild trout.

25% quartile and 75% quartile values for *A. clavula* in wild trout decreased from April to November. The interquartile range increased slightly from April to May and decreased in November (Table 5.5). In stocked trout 25% and 75% quartile values decreased from May to August and increased in November (Table 5.7). The interquartile range for *A. clavula* in stocked trout increased from May to a peak in August and decreased in November. The interquartile range of *A. clavula* was comparable between wild and stocked trout in August, but it considerably smaller in stocked trout in May and considerably larger in November. The interquartile range recorded for *A. clavula* in the total sample was larger in wild trout.

In stocked trout all skewness and kurtosis values were positive and below one, suggesting that the distribution of *A. clavula* in all sample months and for the total sample was peaked and approximated a normal distribution (Table 5.7). In wild trout the skewness value was negative and below one in April, positive and below one in May and August and positive and above one in November. This suggests that the distribution of *A. clavula* approximated a normal distribution in April, May and August but had a positive asymmetric tail in November. Kurtosis values were negative for April, May and August and positive for November, suggesting a flattened distribution in April, May and August and a peaked distribution in November (Table 5.5).

One-way analysis of variance (ANOVA) was used to examine the differences in the distribution of *A. clavula* between wild and stocked trout for each sample month and for the total sample. Significant differences in the distribution of *A. clavula* between wild and stocked trout were shown to exist for the total sample (F ratio = 77.1; df = 1,1171; $p \leq 0.0001$). Significant differences were also shown to exist in the distribution of *A. clavula* between wild and stocked trout for May (F ratio = 66.3; df =

1,427; $p \leq 0.0001$), August (F ratio = 25.2; $df = 1,419$; $p \leq 0.0001$) and November (F ratio = 15.9; $df = 1,263$; $p \leq 0.0001$). The mean position of *A. clavula* was more posterior for wild trout in May, August and for the total sample, and more posterior for stocked trout in August.

5.5.2 *A. clavula* in wild and stocked trout compared by intensity of infection

In this section the distribution of *A. clavula* in low, medium and high intensity infections was compared between wild and stocked trout. Of the 730 *A. clavula* recorded in the total wild trout sample 205 were found in low intensity infections, 324 were found in medium intensity infections and 201 were found in high intensity infections. In stocked trout 126 *A. clavula* were found in low intensity infections, 157 worms were found in medium intensity infections and were found in high intensity infections (Table 5.8).

The mean position of *A. clavula* in wild and stocked trout decreased from low to high intensity infections. In all cases the mean position of *A. clavula* was lower in stocked trout (Table 5.6; Table 5.8).

The median position of *A. clavula* in wild trout decreased from low to medium intensity infections and then increased in high intensity infections (Table 5.6). In stocked trout the median value decreased from low intensity infections to high intensity infections (Table 5.8). The median values recorded for low, medium and high intensity infections in stocked trout were all lower than the corresponding values for wild trout.

The range of occurrence of *A. clavula* in wild trout increased from low to medium intensity infections and subsequently decreased slightly to 69.25% in high intensity infections (Table 5.6). In stocked trout the range of occurrence of *A. clavula* increased from low to medium intensity infections and decreased in high intensity infections (Table 5.8). In all cases the range of occurrence of *A. clavula* was lower in stocked trout.

The interquartile range for *A. clavula* in wild trout increased from low to medium intensity infections and decreased in high intensity infections (Table 5.6), whereas the interquartile range for *A. clavula* in stocked trout decreased from low to medium intensity infections and increased slightly in high intensity infections (Table 5.8). All quartile values were lower in stocked trout. The interquartile ranges of *A. clavula* in low and medium intensity infections were smaller in stocked trout, however the interquartile range of *A. clavula* in high intensity infections was higher in stocked trout.

Skewness values in wild trout were positive and below one in low and medium intensity infections of *A. clavula*, and positive and greater than one in high intensity infections. Kurtosis values were negative in low and medium intensity infections and positive in high intensity infections. This suggests that the distribution of *A. clavula* was slightly flattened but approximated a normal distribution in low and medium intensity infections and was peaked with a positive asymmetric tail in high intensity infections (Table 5.6). In stocked trout skewness values were positive for all intensities and greater than one for medium and high intensities. Kurtosis values were negative for low intensity infections and positive for medium and high intensity infections. This suggests that the distribution of *A. clavula* was flattened but approximated normal in low intensity infections, and peaked with a positive asymmetric tail in medium and high intensity infections (Table 5.8).

The niche width for *A. clavula* was 0.86 for the total sample of wild trout and 0.79 for the total sample of stocked trout. Niche widths were higher for wild trout in May and August, but higher for stocked trout in November. In wild and stocked trout niche width values decreased from low to high intensity infections. They decreased from 0.86 to 0.61 in wild trout, and from 0.80 to 0.54 in stocked trout. For all intensities of infection niche widths were larger in wild trout.

Two-way analysis of variance (ANOVA) was used to examine the differences in distribution in *A. clavula* between wild and stocked trout and for low, medium and

high intensity infections. Significant differences were shown to exist in the distribution of *A. clavula* between wild and stocked trout (F ratio = 59.4; 1,1168; $p \leq 0.0001$). A significant difference also existed in the distribution of *A. clavula* between, low, medium and high intensity infections (F ratio = 37.5; df = 1,1168; $p \leq 0.0001$), however the interaction between fish status (wild or stocked) and infection intensity (low, medium, high) was not significant. In all cases the mean position of *A. clavula* was more posterior in wild trout and more anterior in high intensity infections.

5.6 Examination of the niche overlaps between the four most common species in wild and stocked trout

Niche overlaps of the four most prevalent species in wild and stocked trout in Lough Feeagh were calculated using the Morisita-Horn measure (Magurran, 1998).

5.6.1 Niche overlaps in wild trout

P. laevis and *A. clavula*

The niche overlap value for the total sample was comparable with the value recorded in August (Table 5.9). Overlap values peaked in May and the decreased to their lowest level in November (Table 5.9).

P. laevis and *E. crassum*

The niche overlap value recorded in April was considerably higher than the values reported for any other month or for the total sample (Table 5.9).

P. laevis and *Crepidostomum farionis*

The niche overlap for the total sample was comparable with the value recorded in April. Overlap values were over four times larger in May than in April. Values for August and November were comparable, but still about one third the value of the niche overlap recorded in May (Table 5.9).

A. clavula and *E. crassum*

The niche overlap value for the total sample was slightly higher than the value recorded in August. The highest overlap value for any pair of species for any month was recorded in April. Niche overlap values were comparable between May and November and lower for August (Table 5.9).

A. clavula and *Crepidostomum farionis*

The niche overlap value for the total sample was substantially larger than the peak monthly value. Niche overlap values increased from April and May to a peak in November (Table 5.9).

5.6.2 Niche overlaps in stocked trout

P. laevis and *A. clavula*

Overlap values for each month decreased from May to August and increased to November. Values for May and November were identical, and comparable to the value recorded for the total sample (Table 5.10).

P. laevis and *E. crassum*

The overlap value for the total sample was extremely small. There was no overlap in May. Overlap values increased by a factor of ten from August to November (Table 5.10)

P. laevis and *Crepidostomum farionis*

The total overlap value was intermediate between the values recorded for May and November. Overlap values decreased from a peak in May to August and increased slightly in November (Table 5.10).

A. clavula and *E. crassum*

The total overlap value between these two species was comparable to the overlap value recorded in August. The value recorded in November was substantially smaller and there was no overlap between these two species in May (Table 5.10).

A. clavula and *Crepidostomum farionis*

The overlap value recorded for the total sample was comparable to the value recorded in August. Niche overlap values decreased from May to November (Table 5.10).

5.6.3 Comparison of niche overlap values between wild and stocked trout

The niche overlaps between wild and stocked trout were compared for each of the species pair combinations of the four most prevalent species in Lough Feeagh. Niche overlap values for *P. laevis* and *A. clavula* ranged from 0.13 to 0.44 in wild trout and from 0.06 to 0.38 in stocked trout. Niche overlap values were higher for stocked trout in November and for the total sample.

Niche overlap values for *P. laevis* and *E. crassum* were extremely small. In wild trout overlap values decreased from a peak of 0.40 in April to 0.004 in May, the total overlap value was 0.01. In stocked trout overlap values were equally small, there was no overlap between *P. laevis* and *E. crassum* in May, and the highest overlap value was 0.06, recorded in November.

For *P. laevis* and *Crepidostomum farionis* niche overlap values in wild trout increased from 0.07 in April to a peak of 0.29 in May and decreased in August and November, 0.12 and 0.11 respectively. In stocked trout the highest niche overlap value was recorded in May, 0.33, this decreased to 0.15 in August and increased to 0.21 in November. All overlap values were higher for stocked trout.

There was total niche overlap between *A. clavula* and *E. crassum* for the wild trout sample in April, this value decreased to 0.3 in May and 0.15 in August, it increased again to 0.26 in November. In stocked trout there was no overlap between *A. clavula* and *E. crassum* in May, however the overlap value for August, 0.26 was higher than that recorded for wild trout and the overlap value recorded for November, 0.16 was lower than that recorded for wild trout.

When *A. clavula* and *Crepidostomum farionis* were compared overlap values for wild trout were identical for April and May, 0.02, and increased in August and peaked at 0.35 in November. In stocked trout niche overlap values decreased from a peak of 0.23 in May to 0.12 in November. Niche overlap values for August and November were higher in wild trout.

Table 5.9 Niche overlaps of the four most prevalent parasite species in wild trout in Lough Feeagh, for each monthly sample and the total sample, calculated using the Morisita-Horn quantitative similarity index.

Species	April	May	August	November	Total
<i>P. laevis</i> & <i>A. clavula</i>	0.40	0.44	0.21	0.13	0.23
<i>P. laevis</i> & <i>E. crassum</i>	0.40	0.004	0.07	0.006	0.01
<i>P. laevis</i> & <i>C. farionis</i>	0.07	0.29	0.12	0.11	0.09
<i>A. clavula</i> & <i>E. crassum</i>	1	0.30	0.15	0.26	0.18
<i>A. clavula</i> & <i>C. farionis</i>	0.02	0.02	0.32	0.35	0.56

Table 5.10 Niche overlaps of the four most prevalent parasite species in stocked trout in Lough Feeagh, for each monthly sample and the total sample, calculated using the Morisita-Horn quantitative similarity index.

Species	May	August	November	Total
<i>P. laevis</i> & <i>A. clavula</i>	0.34	0.06	0.34	0.38
<i>P. laevis</i> & <i>E. crassum</i>	0	0.003	0.06	0.05
<i>P. laevis</i> & <i>C. farionis</i>	0.33	0.15	0.21	0.27
<i>A. clavula</i> & <i>E. crassum</i>	0	0.25	0.16	0.27
<i>A. clavula</i> & <i>C. farionis</i>	0.23	0.13	0.12	0.15

5.7 Examination of the distribution of *P. laevis* when it occurred in low, medium and high intensity infections of *A. clavula* in wild trout

The distribution of *P. laevis* was examined when it co-occurred with *A. clavula* in low, medium and high intensity infections (Table 5.11; Fig 5.15). It was also compared to the distribution of *P. laevis* in low, medium and high intensity infections for the total wild trout sample in Lough Feeagh (Table 5.2).

60 *P. laevis* co-occurred with *A. clavula* in low intensity infections, 15 in medium intensity infections and 4 in high intensity infections. The mean position decreased from low to high intensity infections (Table 5.11). For the total sample of *P. laevis* (Table 5.2), the mean position increased from low to medium intensity infections, and decreased from medium to high intensity infections. The mean positions for medium intensity infections were comparable between both groups (Table 5.2; Table 5.11), but the mean position for *P. laevis* in low intensity infections was considerably lower for the total sample (Table 5.2).

Median values for *P. laevis* co-occurring with *A. clavula* decreased from low to high intensity infections (Table 5.11). The median value for *P. laevis* co-occurring with *A. clavula* in low intensity infections was higher than the corresponding value for the total sample (Table 5.2), all other median values for *P. laevis* co-occurring with *A. clavula* were lower.

Minimum values for *P. laevis* increased from low to medium intensity infections of *A. clavula*, and then decreased in high intensity infections of *A. clavula*. They were all substantially higher than the values recorded for the total sample (Table 5.11). Maximum values were comparable for low and medium intensity infections, but substantially lower for high intensity infections of *A. clavula*. Minimum values for *P. laevis* in the total sample decreased from low to high intensity infections (Table 5.2) and, maximum values for the total sample were all comparable.

Correspondingly, the range of occurrence for *P. laevis* co-occurring with *A. clavula* was largest in low intensity infections and decreased in high intensity infections. The small range of occurrence in high intensity infections was attributable to the low maximum and high minimum values recorded (Table 5.11). For the total sample the range of occurrence followed the opposite pattern, increasing from its smallest value in low intensity infections to its largest value in high intensity infections (Table 5.2).

The interquartile range for *P. laevis* co-occurring with *A. clavula* increased from low to medium intensity infections, but then decreased sharply in high intensity infections (Table 5.11). For the total sample the interquartile range for *P. laevis* increased from low to high intensity infections (Table 5.2).

P. laevis co-occurring with *A. clavula*, had a low negative skewness value in low intensity infections. It had a skewness value which was positive and above one in medium intensity infections, suggesting a positive asymmetric tail. A skewness value of zero was recorded for high intensity infections (Fig 5.15). All kurtosis values were negative, suggesting flatter distributions (Table 5.11). For the total sample all skewness values were negative (and below one for medium and high intensity infections) and all kurtosis values were positive. This suggests that the distribution of *P. laevis* in low, medium and high intensity infections was peaked with a negative asymmetric tail.

The niche width of *P. laevis* was calculated when it occurred at low, medium and high intensities of *A. clavula*. The niche width of *P. laevis* was 0.66 in low, 0.45 in medium and 0.18 in high intensity infections of *A. clavula*. The niche widths of *P. laevis* for the total sample were 0.71 for low, 0.68 for medium 0.76 for high intensity infections. In all cases niche width values for *P. laevis* recorded for the total sample were wider than the niche widths recorded for *P. laevis* when it co-occurred with *A. clavula*.

One-way analysis of variance (ANOVA) showed no significant difference in the distribution of *P. laevis* between low, medium and high intensities of *A. clavula*. However least squares difference post hoc tests showed a significant difference in the distribution of *P. laevis* between high and low intensity infections of *A. clavula* ($p = 0.02$).

5.8 Examination of the distribution of *P. laevis* when it occurred in low, medium and high intensity infections of *E. crassum* in wild trout

The distribution of *P. laevis* was examined when it co-occurred with *E. crassum* in low, medium and high intensity infections (Table 5.12; Fig 5.16). It was also compared to the distribution of *P. laevis* in low, medium and high intensity infections in the total sample (Table 5.2). A low intensity infection of *E. crassum* was one worm, a medium intensity infection was two to four worms, and five or more worms was considered a high intensity infection.

7 *P. laevis* co-occurred with *E. crassum* in low intensity infections, 24 in medium intensity infections and 78 co-occurred with *E. crassum* in high intensity infections. The mean position decreased from low to medium intensity infections, and increased again in high intensity infections. The mean positions for *P. laevis* in medium and high intensity infections of *E. crassum* were comparable (Table 5.12). The mean positions recorded for the total sample were all lower than those recorded for *P. laevis* in low, medium and high intensity infections of *E. crassum* (Table 5.2).

Minimum values for *P. laevis* decrease from low to high intensity infections, and maximum values were all around 98% (Table 5.12). For the total sample minimum values followed the same pattern and decreased from low to high intensity infections, maximum values were all around 100%. There was no overlap between the minimum values recorded for the total sample (Table 5.2) and the minimum values for *P. laevis* in low, medium and high intensity infections of *E. crassum*, which were all higher (Table 5.12).

The range of occurrence for the total sample (Table 5.2) and for *P. laevis* in low, medium and high intensity infections of *E. crassum* (Table 5.12) increased from low to high intensity infections. However, the range of occurrence of *P. laevis* for the total sample was consistently higher, and did not overlap with the range of occurrence of *P. laevis* in low, medium and high intensity infections of *E. crassum* (Table 5.2; Table 5.12).

For the total sample the interquartile range increased from low to high intensity infections (Table 5.2). For *P. laevis* co-occurring with *E. clavula* the interquartile range decreased sharply from low to medium intensity infections and then increased in high intensity infections. The interquartile range for *P. laevis* in medium intensity infections in the total sample was higher than the corresponding sample when *P. laevis* co-occurred with *E. crassum*.

P. laevis had negative skewness values for low and high intensity infections of *E. crassum* and a positive skewness value for medium intensity infections. In all cases skewness values were below one suggesting that there was no distinct asymmetric tails. Kurtosis values were positive for medium and high intensity infections of *E. crassum* and negative for low intensity infections. This suggests that the distribution of *P. laevis* was flattened for low intensities of *E. crassum* and somewhat peaked for medium and high intensities of *E. crassum* (Table 5.12). For the total sample all intensities had negative skewness values and positive kurtosis values suggesting relatively peaked distributions with slight negative asymmetrical tails (Table 5.2).

The niche width of *P. laevis* when it co-occurred with *E. crassum* was 0.45 in low, 0.57 in medium and 0.64 in high intensity infections. The niche width of *P. laevis* for the total sample was 0.71 in low, 0.68 in medium and 0.76 in high intensity infections. In all cases the niche widths of *P. laevis* were wider for the total sample. One-way analysis of variance (ANOVA) showed no significant difference in the distribution of *P. laevis* between low, medium and high intensities of *E. crassum*.

Table 5.11 Summary statistics for the distribution of *P. laevis* when it occurs in low (1-15 worms), medium (16-75 worms) and high (76+ worms) intensity infections of *A. clavula* in the intestine of wild trout from Lough Feeagh.

	Low	Medium	High
Count	60	15	4
Mean ($\pm$ S.D.)	84.58($\pm$ 8.75)	81.6($\pm$ 9.36)	71.96($\pm$ 2.26)
Median	85.15	76.71	71.96
Inter quartile	12.68	13.78	3.91
Range			
Minimum	63.93	72.88	70
Maximum	99	99.35	73.91
Range	35.37	26.47	3.91
Skewness	-0.08	1.03	0
Kurtosis	-0.55	-0.57	-2
Lower (25%)	78.92	75.34	70
Upper (75%)	91.6	89.13	73.91

Table 5.12 Summary statistics for the distribution of *P. laevis* when it occurs in low (1 worm), medium (2-4 worms) and high (5+ worms) intensity infections of *E. crassum* in the intestine of wild trout from Lough Feeagh.

	Low	Medium	High
Count	7	24	78
Mean ($\pm$ S.D.)	88.28($\pm$ 9.54)	81.8($\pm$ 7.7)	82.45($\pm$ 8.84)
Median	86.45	81.12	81.85
Inter quartile	17.58	5.79	10.05
Range			
Minimum	75.2	67.05	46.47
Maximum	98.85	98.25	98.94
Range	23.65	31.2	52.47
Skewness	-0.17	0.77	-0.67
Kurtosis	-1.46	0.42	2.42
Lower (25%)	80	77.33	77.45
Upper (75%)	97.57	83.12	87.5

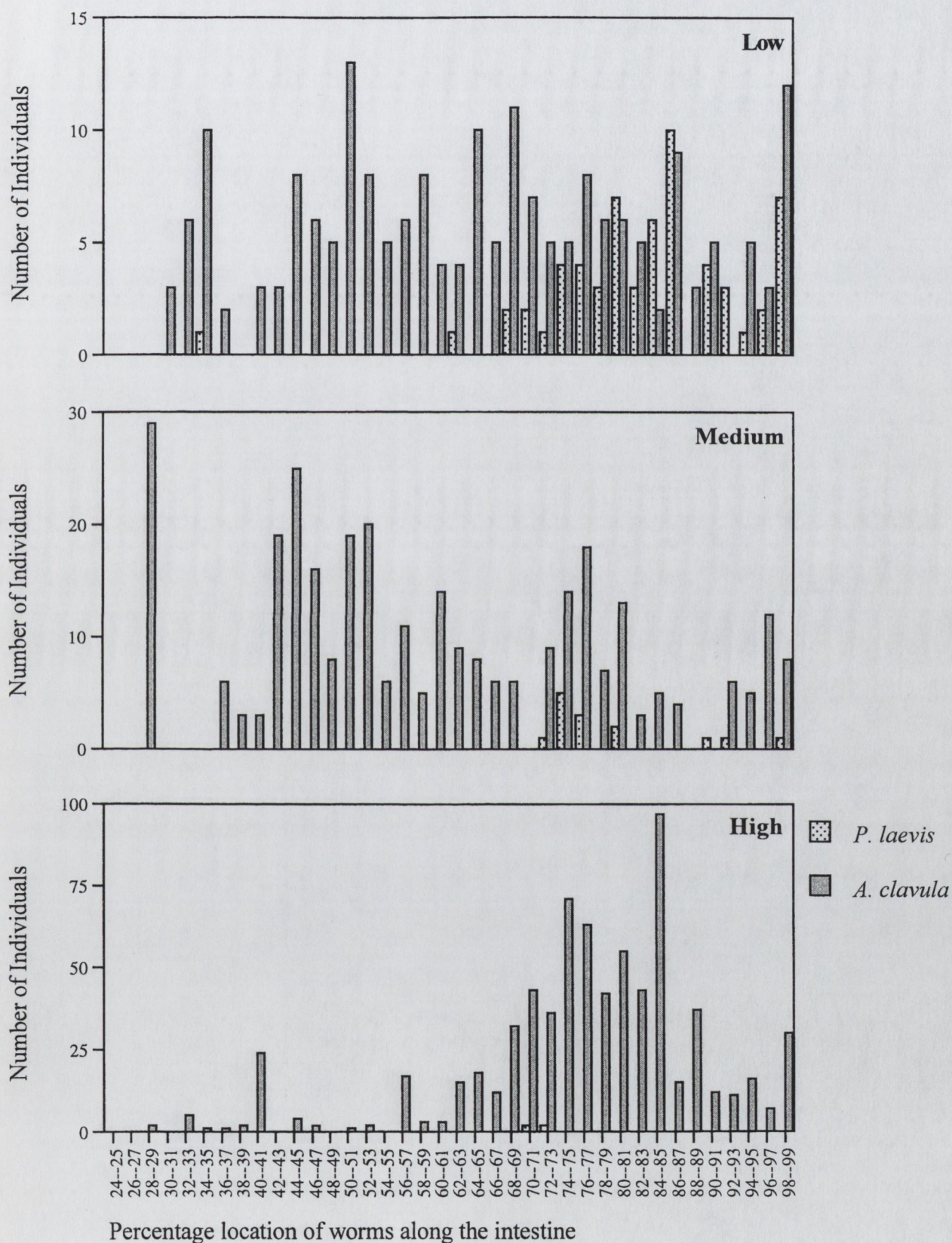


Fig 5.15 Niches of *P. laevis* in low intensity (1-15 worms), medium intensity (16-75 worms), and high intensity (76+ worms) infections of *A. clavula* along the intestine of wild trout in Lough Feeagh.

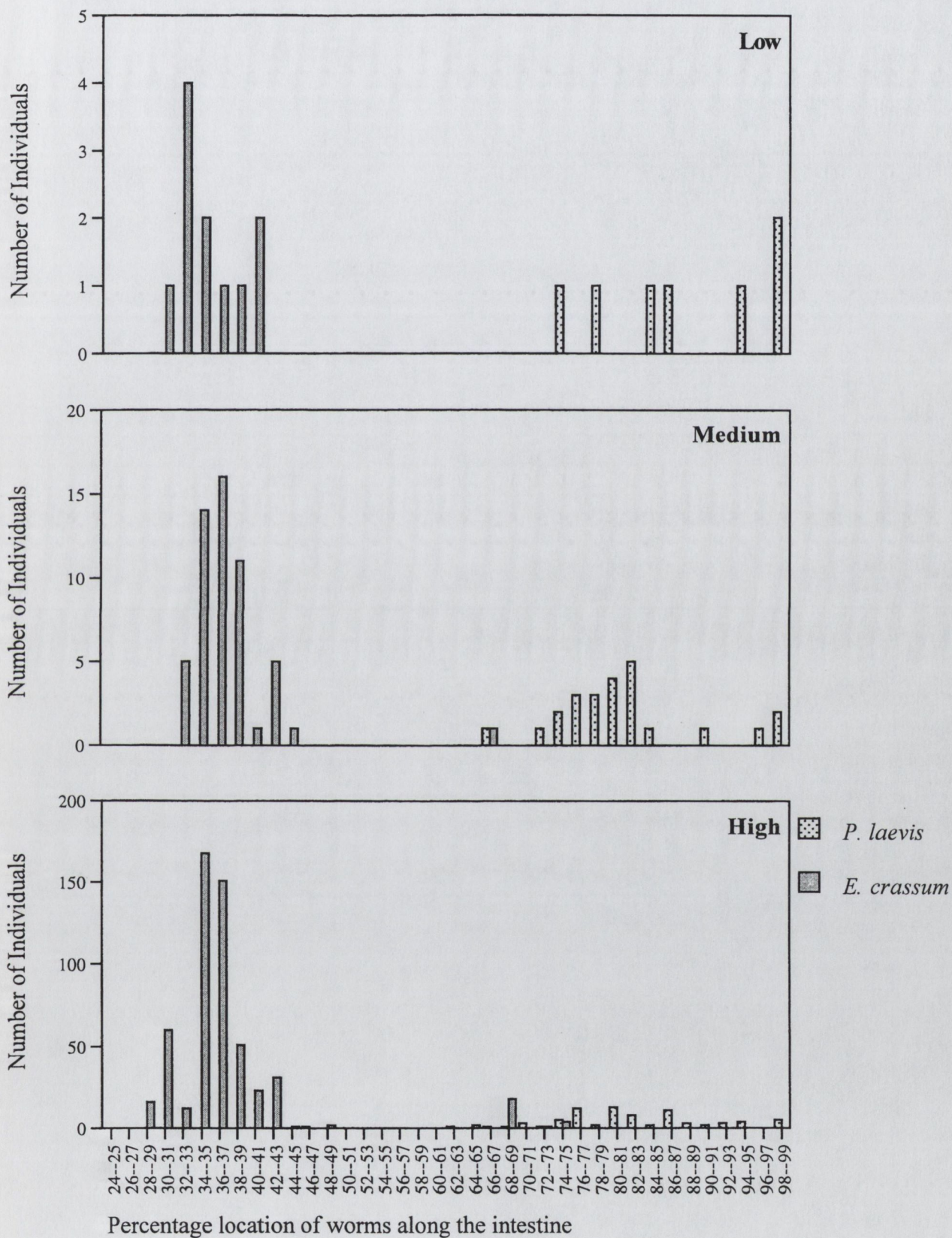


Fig 5.16 Niches of *P. laevis* in low intensity (1 worm), medium intensity (2-4 worms), and high intensity (5+ worms) infections of *E. crassum* along the intestine of wild trout in Lough Feeagh.

5.9 Examination of the distribution of *A. clavula* when it occurred in low, medium and high intensity infections of *P. laevis* in wild trout

In a reversal of the previous section the distribution of *A. clavula* was examined when it co-occurred with *P. laevis* in low, medium and high intensity infections (Table 5.13; Fig 5.17). This was compared to the distribution of *A. clavula* in low, medium and high intensity infections for the total sample (Table 5.6).

A total of 53 *A. clavula* co-occurred with *P. laevis* low intensity infections and 16 *A. clavula* 16 with *P. laevis* in medium and high intensity infections. The mean position decreased from low to medium intensity infections, and then increased again in high intensity infections (Table 5.13). For the total sample of *A. clavula* the mean position decreased from low intensity to high intensity infections (Table 5.6). There was no overlap in the mean positions recorded for *A. clavula* in the total sample and *A. clavula* in low, medium and high intensity infections of *P. laevis*. The mean positions of *A. clavula* in the total sample were consistently lower (Table 5.6).

Median values for *A. clavula* at different intensities of *P. laevis* followed the same pattern as mean values. They decreased from low to medium intensity infections, and then increased in high intensity infections, values for low and high intensity infections were comparable (Table 5.13). For the total sample of *A. clavula* median values decreased from low to medium intensity infections and increased in high intensity infections. The median values for low and high intensity infections were comparable (Table 5.6). In all cases median values recorded for *A. clavula* when it co-occurred with *P. laevis* were higher than median values recorded for *A. clavula* in the total sample.

Minimum values for *A. clavula* when it co-occurred with *P. laevis* increased substantially from low to medium intensity infections and then decreased in high intensity infections. Maximum values were comparable for low and high intensity infections and lower for medium intensity infections. The range of occurrence

followed a similar pattern decreasing from low to medium intensity infection and then increasing in high intensity infections (Table 5.13). For the total sample of *A. clavula* minimum and maximum values decreased from low to medium intensity infections and increased slightly in high intensity infections. The range of occurrence of *A. clavula* for the total sample varied by only 1.45% between the smallest and the largest values (Table 5.6). In all cases the range of occurrence for *A. clavula* in the total sample was higher than the range of occurrence recorded for *A. clavula* when it co-occurred with *P. laevis*.

When *A. clavula* co-occurred with *P. laevis* the interquartile range decreased in size from low to high intensity infections (Table 5.13). For the total sample the interquartile range increased from low to medium intensity and decreased sharply in high intensity infections (Table 5.6). There was some overlap in the interquartile ranges for the total sample of *A. clavula* and *A. clavula* at different intensities of *P. laevis*.

Skewness values for low and high intensity infections were negative, and skewness values for all three intensities of *P. laevis* were below one. All kurtosis values were negative. This suggests that for all three intensities of *P. laevis*, *A. clavula* had a slightly flattened distribution which approximated normal (Table 5.13; Fig 5.17). For the total sample skewness values were all positive. They were below one for low and medium intensity infections. Kurtosis values for low and medium intensity infections were negative. This suggested that low and medium intensity infections of *A. clavula* for the total sample had flattened a distribution which approximated normal, and high intensity infections had a peaked distribution with a positive asymmetric tail (Table 5.6).

The niche width of *A. clavula* was 0.79 at low intensities of *P. laevis*, 0.55 at medium intensities and 0.57 at high intensities of *P. laevis*. The niche width of *A. clavula* for the total sample was 0.86 in low intensity infections, 0.82 in medium intensity infections and 0.61 in high intensity infections. The niche width of *A. clavula* was

considerably wider for low and medium and high intensity infections for the total sample. One-way analysis of variance (ANOVA) showed no significant difference in the distribution of *A. clavula* between low, medium and high intensity infections of *P. laevis*.

5.10 Examination of the distribution of *A. clavula* when it occurred in low, medium and high intensity infections of *E. crassum* in wild trout

The distribution of *A. clavula* was examined when it co-occurred with *E. crassum* in low, medium and high intensity infections (Table 5.14; Fig 5.18) and this was compared to the distribution of *A. clavula* in low, medium and high intensity infections for the total sample (Table 5.6). A low intensity infection of *E. crassum* was one worm, two to four worms was a medium intensity infection and five or more worms was considered to be a high intensity infection of *E. crassum*.

A total of 4 *A. clavula* were found in low intensity infections of *E. crassum*, 13 were found in medium intensity infections and 64 were found in high intensity infections. The mean position decreased from medium to high intensity infections, low intensity infections had an intermediate mean position value (Table 5.14). The opposite pattern was observed for *A. clavula* in the total sample. The mean position was highest in high intensity infections and lowest in medium intensity infections (Table 5.6). The highest mean position value for the total sample of *A. clavula* was nearly identical to the lowest mean position value for *A. clavula* at different intensities of *E. crassum*.

Median values followed the same pattern as mean values increasing substantially from low to medium intensity infections and decreasing to their lowest value in high intensity infections (Table 5.14). For the total sample of *A. clavula* median values were lowest for medium intensity infections and comparable for low and high intensity infections (Table 5.6). Median values were higher for *A. clavula* co-occurring with *E. crassum* in low and medium intensity infections.

Minimum values were similar for low and medium intensity infections and substantially lower for high intensity infections. Maximum values were comparable in all cases. Correspondingly the range of occurrence of *A. clavula* increased from low to high intensity infections of *E. crassum* (Table 5.14). For the total sample both the minimum and maximum values for low, medium and high intensity infections were comparable. Thus the range of occurrence of *A. clavula* was quite consistent between low, medium and high intensity infections (Table 5.6). In all cases the range of occurrence was larger for *A. clavula* in the total sample.

The interquartile range for *A. clavula* co-occurring with *E. crassum* decreased from low to high intensity infections (Table 5.14). For the total sample of *A. clavula* the interquartile range was quite comparable for low and medium intensity infections and substantially smaller for high intensity infections. The interquartile range was higher for *A. clavula* co-occurring with *E. clavula* in low and high intensity infections.

A. clavula had positive skewness values in low and high intensity infections of *E. crassum*, and a negative skewness value in medium intensity infections of *E. crassum*. All skewness values were below one. Kurtosis values for *A. clavula* at all intensities of *E. crassum* were negative. This suggested that for all intensities of *E. crassum*, *A. clavula* had a flattened distribution, which approximated normal (Table 5.14). A similar type distribution, flattened with no obvious asymmetric tails was found for low and medium intensity infections of *A. clavula* in the total sample. For high intensity infections *A. clavula* had a more peaked distribution with a positive asymmetric tail tending towards positive values (Table 5.6).

The niche width of *A. clavula* was 0.35 for low intensity infections of *E. crassum*, 0.41 for medium intensity infections and 0.8 for high intensity infections of *E. crassum*. Niche width values for the total sample of *A. clavula* were 0.86 for low, 0.82 for medium and 0.61 for high intensity infections. In all cases niche width values were considerably higher for *A. clavula* in the total sample. One-way analysis of variance (ANOVA) showed significant differences in the distribution of *A. clavula*

between low, medium and high intensities of *E. crassum* (F ratio = 3.8; df = 2,31; p = 0.03). Least squares difference post hoc tests showed a significant difference in the distribution of *A. clavula* between high and medium intensities of *E. crassum* (p = 0.01).

Table 5.13 Summary statistics for the distribution of *A. clavula* when it occurs in low (1-5 worms), medium (6-9 worms) and high (10+ worms) intensity infections of *P. laevis* in the intestine of wild trout from Lough Feeagh.

	Low	Medium	High
Count	53	16	16
Mean ($\pm$ S.D.)	74.43($\pm$ 19.05)	68.4($\pm$ 14.54)	73.12($\pm$ 17.43)
Median	77.77	69.6	76.6
Inter quartile	32.3	23.73	21.17
Range			
Minimum	31.25	47.3	40.7
Maximum	99.39	95.21	99.23
Range	68.14	47.91	58.53
Skewness	-0.52	0.12	-0.29
Kurtosis	-0.75	-0.96	-0.57
Lower (25%)	55.6	54.35	60.5
Upper (75%)	90.9	78.08	81.67

Table 5.14 Summary statistics for the distribution of *A. clavula* when it occurs in low (1 worm), medium (2-4 worms) and high (5+ worms) intensity infections of *E. crassum* in the intestine of wild trout from Lough Feeagh.

	Low	Medium	High
Count	4	13	64
Mean ($\pm$ S.D.)	77.71($\pm$ 19.51)	86.16($\pm$ 16.66)	64.67($\pm$ 15.79)
Median	76.16	92.95	62.14
Inter quartile	32.39	27.48	21.03
Range			
Minimum	58.51	56.16	33.33
Maximum	100	99.32	98.1
Range	41.49	43.16	64.77
Skewness	0.14	-0.95	0.45
Kurtosis	-1.69	-0.77	-0.49
Lower (25%)	61.51	70.99	53.58
Upper (75%)	93.9	98.48	74.61

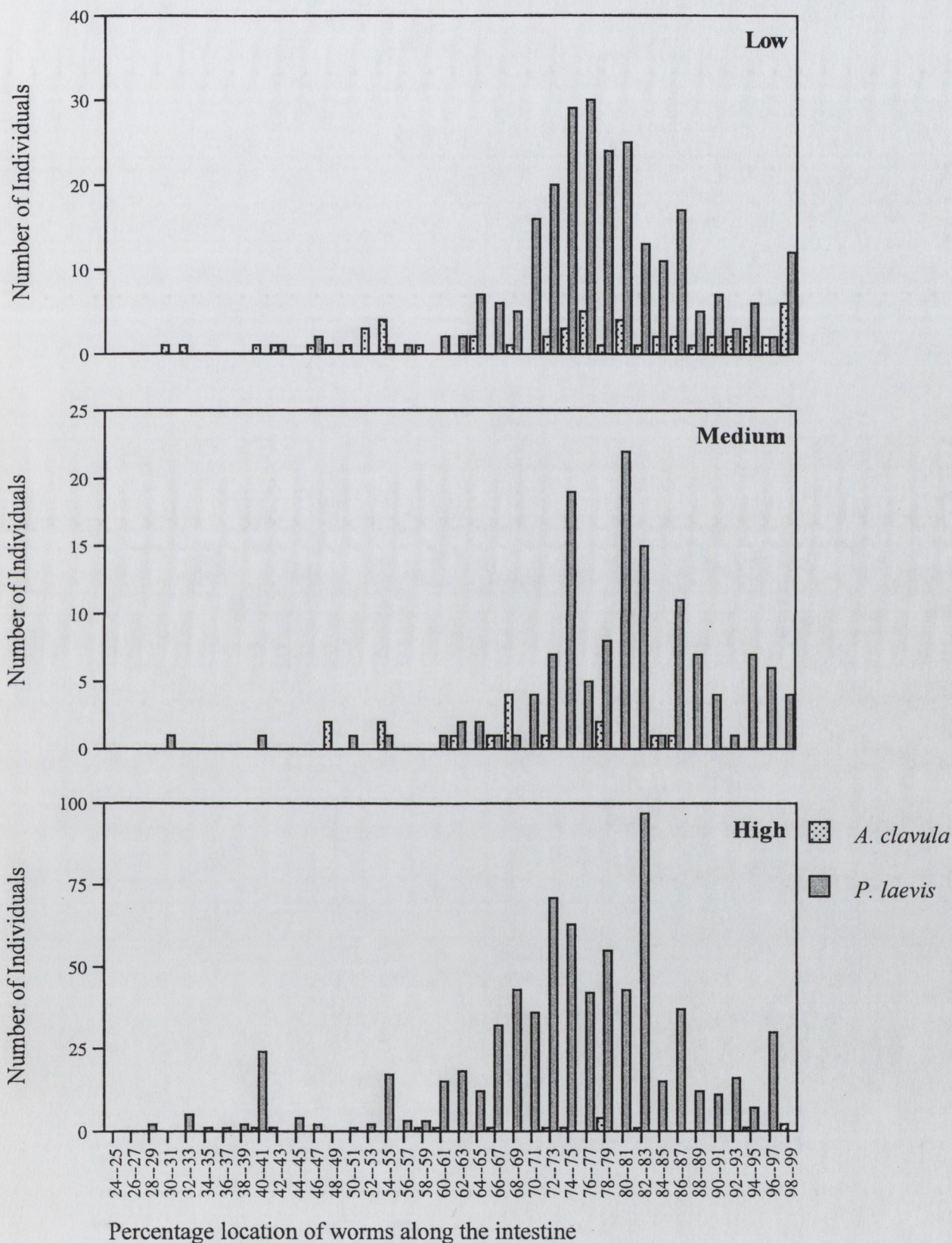


Fig 5.17 Niches of *A. clavula* in low intensity (1-5 worm), medium intensity (6-9 worms), and high intensity (10+ worms) infections of *P. laevis* along the intestine of wild trout in Lough Feeagh.

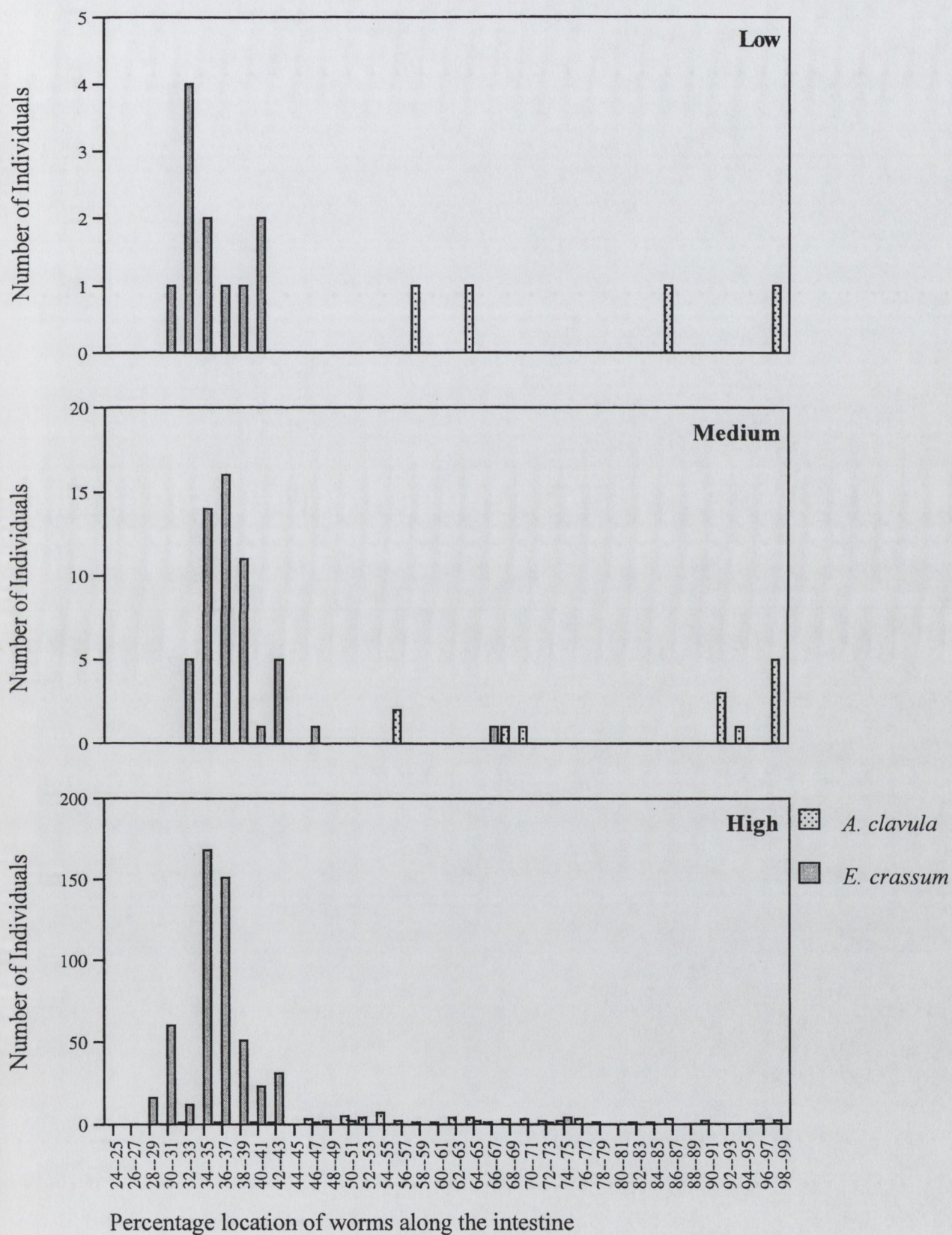


Fig 5.18 Niches of *A. clavula* in low intensity (1 worm), medium intensity (2-4 worms), and high intensity (5+ worms) infections of *E. crassum* along the intestine of wild trout in Lough Feeagh.

5.11 Examination of the distribution of *P. laevis* when it occurred in low, medium and high intensity infections of *A. clavula* in stocked trout

The distribution of *P. laevis* was examined when it occurred in low, medium and high intensity infections of *A. clavula* in stocked trout in Lough Feeagh (Table 5.15; Fig 5.19). It was also compared to the distribution of *P. laevis* in low, medium and high intensity for the total sample (Table 5.4).

34 *P. laevis* were found in low intensity infections of *A. clavula*, 18 were found in medium intensity infections and one worm was found in high intensity infections of *A. clavula* (Table 5.15). The mean position decreased from low to medium intensity infections. *P. laevis* in high intensity infections had an intermediate mean position.

Median values also decreased from low to medium intensity infections. The mean, median, minimum, maximum and 25% and 75% quartile values were all 62.25% for high intensity infections. The mean and median values recorded for *P. laevis* in low intensity infections of *A. clavula* were higher than the values recorded for the low intensity infections for the total sample of *P. laevis*. The mean and median values recorded for *P. laevis* in medium intensity infections of *A. clavula* were substantially smaller than any values recorded for the total sample (Table 5.4).

Minimum values decreased substantially from low to medium intensity infections. Maximum values also decreased from low to medium intensity infections, although the reduction was not as large as recorded for minimum values (Table 5.15). Correspondingly, the range of occurrence of *P. laevis* increased from low to medium intensity infections. The range of occurrence recorded for low and medium intensity infections of *P. laevis* in the total sample (Table 5.4) was considerably higher than the range of occurrence recorded for *P. laevis* when it co-occurred with *A. clavula*.

The interquartile range for *P. laevis* co-occurring with *A. clavula* increased substantially from low to medium intensity infections (Table 5.15). The interquartile

range recorded for the total sample of *P. laevis* increased from low to medium intensity infections and decreased in high intensity infections (Table 5.4). The largest interquartile range recorded for the total sample of *P. laevis* (Table 5.4) was smaller than the smallest interquartile range recorded for *P. laevis* in the presence of *A. clavula* (Table 5.15).

Skewness values for low and medium intensity infections were positive and below one and kurtosis values were negative. This suggests that *P. laevis* had a slightly flattened distribution with no obvious asymmetric tails when it occurred in low and medium intensity infections of *A. clavula*. All skewness values for *P. laevis* in the total sample were negative and below one and kurtosis values for low and high intensity infections were positive. This suggests that the distribution of *P. laevis* in the total sample approximated a normal distribution but was slightly peaked for low and high intensity infections and slightly flattened for medium intensity infections.

The niche width of *P. laevis* was 0.62 in low intensity infections, 0.66 in medium intensity infections and zero for high intensity infections of *A. clavula*. For the total sample of *P. laevis* the niche width was 0.75 in low intensity infections, 0.74 in medium intensity infections and 0.76 in high intensity infections. In all cases niche widths of *P. laevis* recorded for the total sample were wider than the niche widths recorded for *P. laevis* in low, medium and high intensity infections of *A. clavula*.

One-way analysis (ANOVA) of variance showed a significant difference in the distribution of *P. laevis* between low, medium and high intensity infections of *A. clavula* (F ratio = 20.5; df = 2,50; $p \leq 0.0001$). Least squares difference post hoc tests showed a significant difference in the distribution of *P. laevis* between medium and low intensity infections of *A. clavula* ($p \leq 0.0001$).

5.12 Examination of the distribution of *P. laevis* when it occurred in low, medium and high intensity infections of *E. crassum* in stocked trout

The distribution of *P. laevis* was examined when it occurred in low, medium and high intensity infections of *E. crassum* (Table 5.16; Fig 5.20). This was then compared to the total sample of *P. laevis* in low, medium and high intensity infections (Table 5.4).

4 *P. laevis* co-occurred with *E. crassum* in low intensity infections, 25 co-occurred in medium intensity infections and 142 co-occurred with *E. crassum* in high intensity infections. The mean position increased from low to medium intensity infections and then decreased high intensity infections. In the total sample the mean location of *P. laevis* decreased from low to medium intensity infections (Table 5.4). In all cases the mean positions recorded for *P. laevis* when it co-occurred with *E. crassum* were higher than the mean positions recorded for the total sample of *P. laevis* (Table 5.4; Table 5.16).

Median values decreased from low to high intensity infections of *E. crassum* (Table 5.16). For the total sample of *P. laevis* median values were nearly identical for low and medium intensity infections and decreased slightly in high intensity infections (Table 5.4). In all cases median values were higher for *P. laevis* when it co-occurred with *E. crassum*.

Minimum values decreased substantially from low to high intensity infections of *E. crassum*, whereas maximum values increased from low to high intensity infections (Table 5.16). Correspondingly, the range of occurrence for *P. laevis* more than doubled from low to high intensity infections of *E. crassum*. For the total sample of *P. laevis* minimum and maximum values were reasonably consistent. However, the range of occurrence increased from low to medium intensity infections and decreased in high intensity infections (Table 5.4). In all cases the range of occurrence was highest for *P. laevis* in the total sample.

The interquartile range increased low to medium intensity infections and then decreased high intensity infections (Table 5.16). The interquartile range for the total sample of *P. laevis* increased from low to medium intensity infections and decreased in high intensity infections (Table 5.4). Although the interquartile ranges were somewhat comparable between the two samples, the 25% and 75% quartile values were all higher for *P. laevis* co-occurring with *E. crassum* (Table 5.16).

P. laevis co-occurring with *E. crassum* in low and medium intensity infections, had similar flattened distribution which approximated normal. *P. laevis* in high intensity infections of *E. crassum* had positive kurtosis and skewness values suggesting a more peaked distribution which approximated normal (Table 5.16; Fig 5.20). The distribution of *P. laevis* in low and high intensity infections in the total sample was peaked but still approximated normal. In medium intensity infections of *P. laevis* the distribution was slightly flattened but also approximated a normal (Table 5.4).

The niche width of *P. laevis* increased from 0.35 in low intensity infections to 0.65 in medium intensity infections and peaked at 0.70 in high intensity infections of *E. crassum*. The niche widths of *P. laevis* in the total sample were 0.75 for low, 0.74 for medium and 0.76 for high intensity infections.

One-way analysis of variance (ANOVA) showed a significant difference in the distribution of *P. laevis* between low, medium and high intensity infections of *E. crassum* (F ratio = 5.6; df = 2, 168; $p \leq 0.004$). Least squares difference post hoc tests showed a significant difference in the distribution of *P. laevis* between high and medium intensity infections of *E. crassum* ($p \leq 0.001$).

Table 5.15 Summary statistics for the distribution of *P. laevis* when it occurs in low (1-15 worms), medium (16-75 worms) and high (76+ worms) intensity infections of *A. clavula* in the intestine of stocked trout from Lough Feeagh.

	Low	Medium	High
Count	34	18	1
Mean ($\pm$ S.D.)	78.74($\pm$ 8.58)	57.75($\pm$ 15.32)	62.25($\pm$ 0)
Median	80.55	55.5	62.25
Inter quartile	15.35	25.98	0
Range			
Minimum	64.93	37.24	62.25
Maximum	98.85	86.11	62.25
Range	33.92	48.87	0
Skewness	0.02	0.35	-1
Kurtosis	-0.72	-1.07	-2
Lower (25%)	69.12	47.22	62.25
Upper (75%)	84.47	73.2	62.25

Table 5.16 Summary statistics for the distribution of *P. laevis* when it occurs in low (1 worm), medium (2-4 worms) and high (5+ worms) intensity infections of *E. crassum* in the intestine of stocked trout from Lough Feeagh.

	Low	Medium	High
Count	4	25	142
Mean ($\pm$ S.D.)	80.53($\pm$ 9.7)	83.46($\pm$ 9.64)	76.83($\pm$ 9.17)
Median	82.1	80.92	76.47
Inter quartile	15.93	17.42	11.51
Range			
Minimum	68.83	64.47	53.45
Maximum	89.1	99.14	98.85
Range	20.27	34.67	45.4
Skewness	-0.27	0.23	0.09
Kurtosis	-1.63	-0.94	0.16
Lower (25%)	72.57	76.5	71.12
Upper (75%)	88.50	93.92	82.63

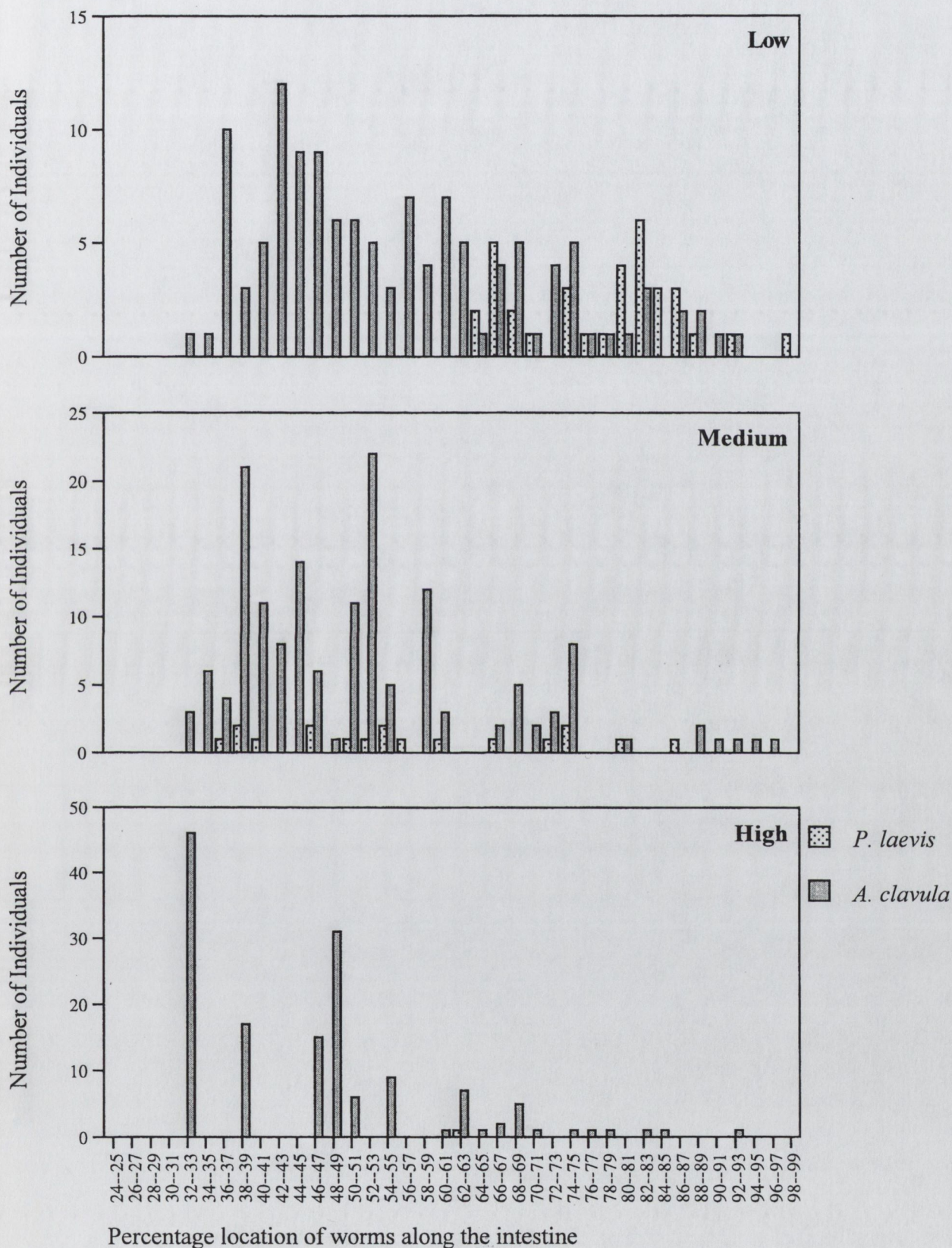


Fig 5.19 Niches of *P. laevis* in low intensity (1-15 worms), medium intensity (16-75 worms), and high intensity (76+ worms) infections of *A. clavula* along the intestine of stocked trout in Lough Feeagh.

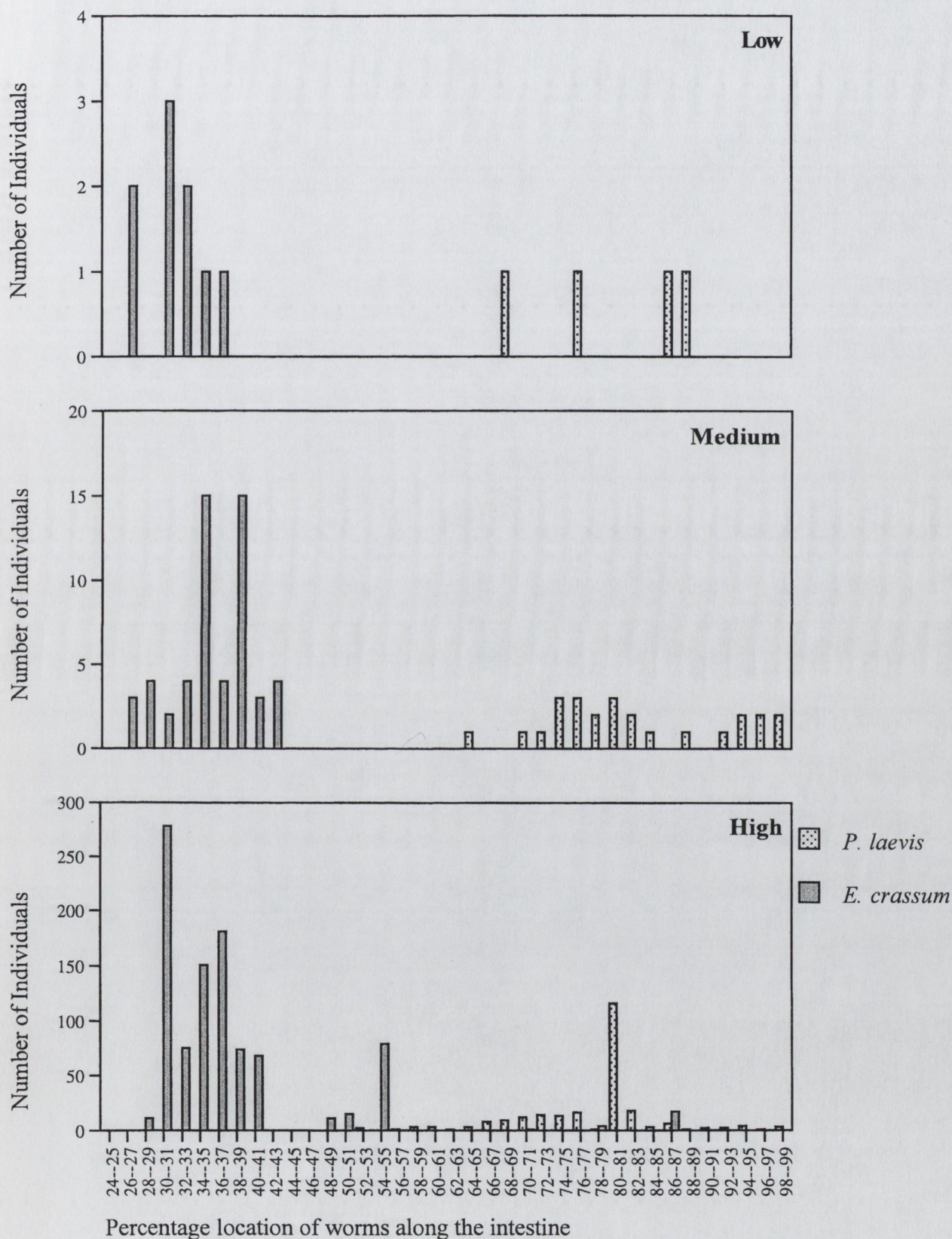


Fig 5.20 Niches of *P. laevis* in low intensity (1 worm), medium intensity (2-4 worms), and high intensity (5+ worms) infections of *E. crassum* along the intestine of stocked trout in Lough Feeagh.

5.13 Examination of the distribution of *A. clavula* when it occurred in low, medium and high intensity infections of *P. laevis* in stocked trout

The distribution of *A. clavula* was examined when it co-occurred with *P. laevis* in low, medium and high intensity infections (Table 5.17; Fig 5.21). The distribution of *A. clavula* when it co-occurred with *P. laevis* was also compared to the distribution of *A. clavula* in low, medium and high intensity infections in the total sample (Table 5.8).

21 *A. clavula* co-occurred with *P. laevis* in low intensity infections, 14 in medium intensity infections and 18 *A. clavula* co-occurred with *P. laevis* in high intensity infections (Table 5.17). The mean position of *A. clavula* decreased from low to high intensity infections of *P. laevis*. In the total sample of *A. clavula* the mean position also decreased from low to high intensity infections (Table 5.8). The lowest mean position value for *A. clavula* in high intensity infections of *P. laevis* was higher than the highest mean position value for *A. clavula* in the total sample (Table 5.17; Table 5.8).

Median values for *A. clavula* decreased from low to high intensity infections of *P. laevis* (Table 5.17). Median values for the total sample of *A. clavula* also decreased from low to high intensity infections (Table 5.8). The lowest median value recorded for *A. clavula* when it co-occurred with *P. laevis* was higher than the highest median value recorded for the total sample (Table 5.8; Table 5.17).

Thus the range of occurrence of *A. clavula* decreased from low to medium intensity infections of *P. laevis* and increased slightly in high intensity infections of *P. laevis* (Table 5.17). The range of occurrence of *A. clavula* for the total sample was also comparable between low, medium and high intensity infections.

The interquartile range for *A. clavula* when it co-occurred with *P. laevis* decreased substantially from low to medium intensity infections and then almost doubled in size

in high intensity infections (Table 5.17). For the total sample of *A. clavula* the interquartile range decreased from low to medium intensity infections, but increased again in high intensity infections (Table 5.8). The interquartile range was substantially higher for *A. clavula* when it co-occurred with *P. laevis* in high intensity infections than for the total sample.

Kurtosis values were negative for *A. clavula* in low, medium and high intensity infections of *P. laevis*. Skewness values were negative for low and medium intensity infections of *P. laevis* and positive for high intensity infections. In all cases skewness values were lower than one. This would suggest that the distribution of *A. clavula* in low, medium and high intensity infections of *P. laevis* was flattened and approximated a normal distribution (Table 5.17; Fig 5.21). For low intensity infections in the total sample *A. clavula* had a flattened distribution which approximated normal, and for medium and high intensity infections it had a peaked distribution with positive asymmetric tail (Table 5.8).

Niche widths for *A. clavula* co-occurring with *P. laevis* were 0.66 in low, 0.60 in medium and 0.66 in high intensity infections. For the total sample of *A. clavula* niche widths decreased from 0.80 in low intensity infections to 0.72 in medium intensity infections and 0.54 in high intensity infections. The niche widths recorded for *A. clavula* in low, medium and high intensity infections of *P. laevis* were within the range of niche width values recorded for the total sample.

One-way analysis of variance (ANOVA) showed no significant difference in the distribution of *A. clavula* between low, medium and high intensity infections of *P. laevis*.

5.14 Examination of the distribution of *A. clavula* when it occurred in low, medium and high intensity infections of *E. crassum* in stocked trout

The distribution of *A. clavula* was examined when it co-occurred with *E. crassum* in low, medium and high intensity infections (Table 5.18; Fig 5.22). This was then compared to *A. clavula* in low, medium and high intensity infections in the total sample (Table 5.8).

7 *A. clavula* co-occurred with *E. crassum* in low intensity infections, 8 in medium intensity infections and 102 *A. clavula* co-occurred with *E. crassum* in high intensity infections. The mean position decreased from low to medium intensity infections and increased in high intensity infections (Table 5.18). For the total sample of *E. crassum* mean positions decreased from low to high intensity infections (Table 5.8). In all cases mean positions for *A. clavula* were higher when it co-occurred with *E. crassum* than for the total sample (Table 5.18; Table 5.8).

Median values for *A. clavula* co-occurring with *E. crassum* followed the same pattern as mean values, decreasing from a peak in low intensity infections to their lowest value in medium intensity infections and then increasing again in high intensity infections (Table 5.18). For the total sample of *A. clavula* median values decreased from low to high intensity infections (Table 5.8). Median values recorded for *A. clavula* in low, medium and high intensity infections of *E. crassum* were within the range of median values recorded for the total sample (Table 5.18; Table 5.8).

The range of occurrence of *A. clavula* decreased from low to medium intensity infections and increased to a peak in high intensity infections of *E. crassum* (Table 5.18). Minimum and maximum values for the total sample of *A. clavula* were consistent and varied by only about 4%. The range of occurrence of *A. clavula* for the total sample was equally consistent and decreased from a peak in medium intensity infections to its lowest value in high intensity infections (Table 5.8). *A. clavula* in the

total sample had a higher range of occurrence in low and medium intensity infections (Table 5.8).

The interquartile range for *A. clavula* when it co-occurred with *E. crassum* reflected the same variable pattern as the 75% quartile values, decreasing low to medium intensity infections and then increasing again high intensity infections (Table 5.18). The interquartile range for the total sample of *A. clavula* also peaked in low intensity infections and was smallest in medium intensity infections. The interquartile range of *A. clavula* in medium and high intensity infections of *E. crassum* were lower than any interquartile range values recorded in the total sample.

The distribution of *A. clavula* in low intensity infections of *E. crassum* was slightly flattened but approximated a normal distribution. For medium and high intensity infections of *E. crassum* the distribution of *A. clavula* was peaked and had a positive asymmetrical tail (Table 5.18; Fig 5.22). The same patterns of distribution were found for *A. clavula* in low, medium and high intensity infections in the total sample (Table 5.8) as were found for *A. clavula* in low, medium and high intensity infections of *E. crassum* (Table 5.18).

Niche widths for *A. clavula* were 0.50 in low, 0.35 in medium and 0.72 in high intensity infections of *E. crassum*. Niche widths for *A. clavula* in the total sample were 0.80 in low, 0.72 in medium and 0.54 in high intensity infections. One-way analysis (ANOVA) of variance showed no significant difference in the distribution of *A. clavula* between low, medium and high intensity infections of *E. crassum*.

Table 5.17 Summary statistics for the distribution of *A. clavula* when it occurs in low (1-5 worms), medium (6-9 worms) and high (10+ worms) intensity infections of *P. laevis* in the intestine of stocked trout from Lough Feeagh.

	Low	Medium	High
Count	21	14	18
Mean ($\pm$ S.D.)	66.34($\pm$ 18.72)	64.82($\pm$ 15.49)	57.29($\pm$ 16.48)
Median	75.86	66.69	59.87
Inter quartile	28.78	16.31	30.54
Range			
Minimum	32.55	37.22	33.3
Maximum	95.42	90	89.28
Range	62.87	52.78	55.98
Skewness	-0.19	-0.14	0.31
Kurtosis	-1.27	-0.33	-1.07
Lower (25%)	49.11	57.06	41.66
Upper (75%)	77.89	73.37	72.2

Table 5.18 Summary statistics for the distribution of *A. clavula* when it occurs in low (1 worm), medium (2-4 worms) and high (5+ worms) intensity infections of *E. crassum* in the intestine of stocked trout from Lough Feeagh.

	Low	Medium	High
Count	7	8	102
Mean ($\pm$ S.D.)	60.7($\pm$ 20.87)	55.3($\pm$ 14.51)	56.4($\pm$ 12.58)
Median	56.96	46.64	53.59
Inter quartile	28.71	9.82	11.9
Range			
Minimum	32.55	46.7	33.98
Maximum	93.6	89.28	95.42
Range	51.05	42.58	61.44
Skewness	0.39	1.86	1.28
Kurtosis	-0.89	1.98	1.43
Lower (25%)	47.96	47.84	49.54
Upper (75%)	76.66	57.21	61.44

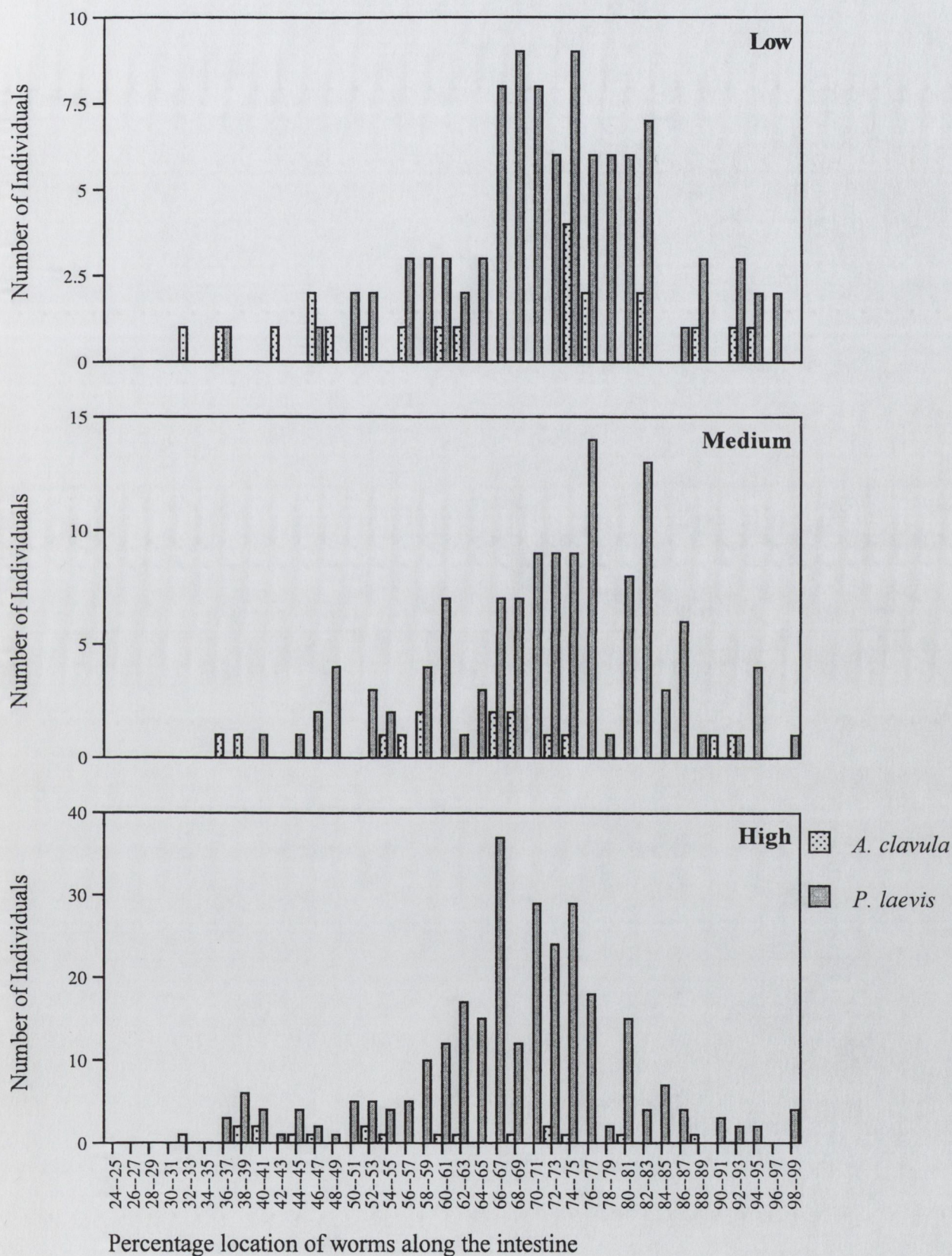


Fig 5.21 Niches of *A. clavula* in low intensity (1-5 worm), medium intensity (6-9 worms), and high intensity (10+ worms) infections of *P. laevis* along the intestine of stocked trout in Lough Feeagh.

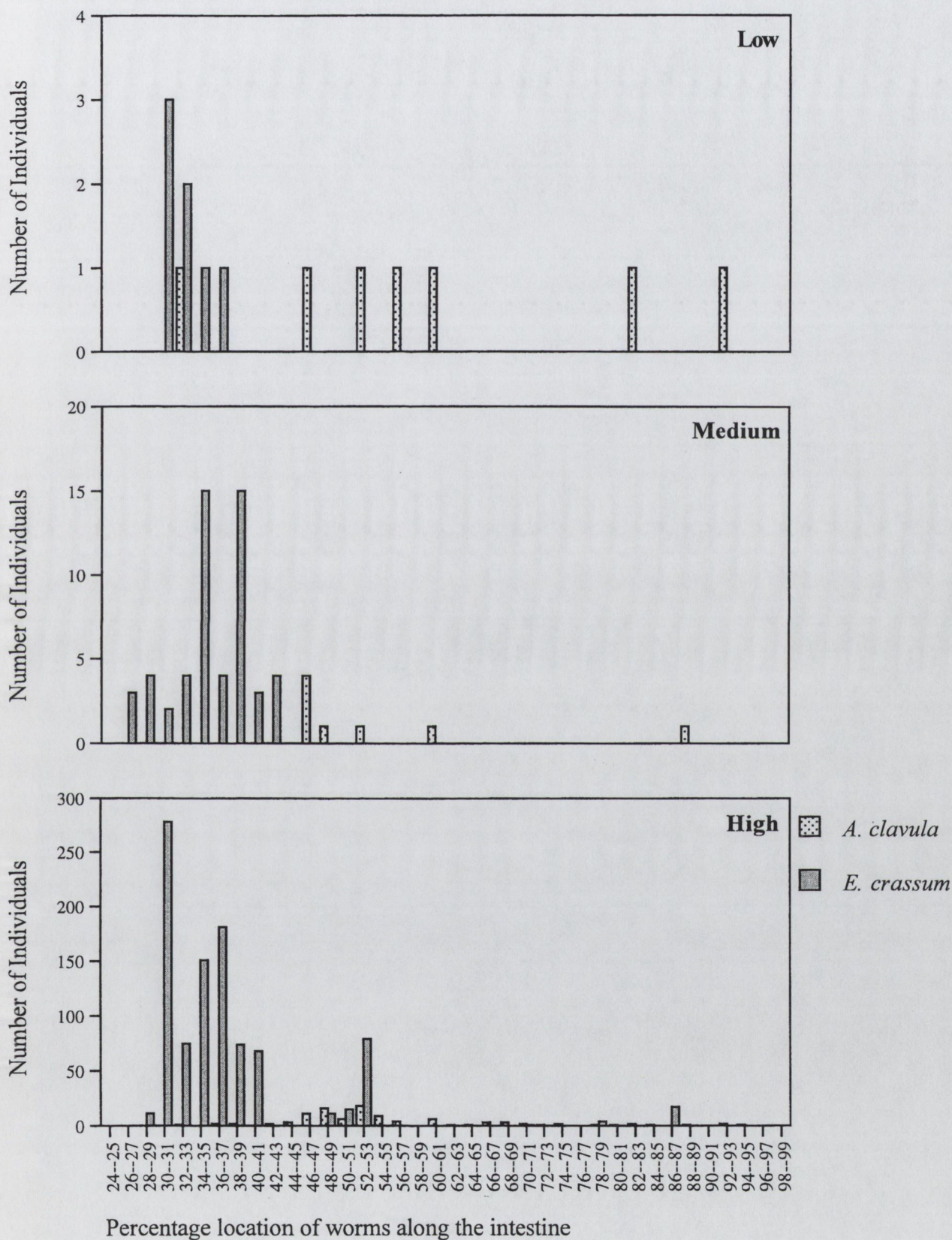


Fig 5.22 Niches of *A. clavula* in low intensity (1 worm), medium intensity (2-4 worms), and high intensity (5+ worms) infections of *E. crassum* along the intestine of stocked trout in Lough Feeagh.

5.15 Discussion

Q. Is the niche of *P. laevis* typical?

Conneely and McCarthy (1988) and Fitzgerald and Mulcahy (1983) provided some information on the site selection of male and female *P. laevis* in the intestine of brown trout in Ireland. However, only Molloy *et al.* (1995b) examined the population biology and microhabitat selectivity of the Irish strain of *P. laevis* in any detail. However no studies to date have compared the microhabitat selectivity of *P. laevis* in wild and stocked trout.

For the total wild brown trout sample *P. laevis* occupied a posterior position in the intestine and its distribution was peaked with an anterior asymmetric tail. Although the preferred position of *P. laevis* was more posterior, worms were recorded all along the intestine. The distribution of *P. laevis* in each monthly sample followed a similar pattern. However, the mean position recorded for *P. laevis* shifted in an anterior direction from April to November. The niche width value for the total sample was comparable to the values recorded in each of the monthly samples.

A similar distribution was reported for *P. laevis* in low, medium and high intensity infections. The most posterior mean position was recorded for *P. laevis* in medium intensity infections and the most anterior mean position was recorded for *P. laevis* in high intensity infections. The niche width value increased from medium to high intensity infections. Thus, it can be concluded that *P. laevis* preferably occupied a posterior position along the alimentary tract of trout, but site fidelity in individual fish was poor as worms were found all along the intestine.

Molloy *et al.* (1995b) reported similar findings for the location of *P. laevis* along the intestine of brown trout from Lough Feeagh. They examined the population biology and microhabitat selectivity of 731 *P. laevis* from brown trout in Lough Feeagh and reported an overall mean position of 77%, a value almost identical to the total mean

position value reported for this study, 78%. They also demonstrated that the distribution of *P. laevis* was peaked with an anterior asymmetric tail. Fitzgerald and Mulcahy (1983) demonstrated that unattached *P. laevis* occurred all along the intestine of trout, but attached *P. laevis* preferentially occurred in the 50-60% region of the intestine. 50-60% of the distance from the pyloric caeca to the anus (as recorded by Fitzgerald and Mulcahy, 1983) corresponds roughly to about 75-85% of the distance from the oesophagus to the anus, which is comparable to the mean position recorded for *P. laevis* in this study. Thus, it can be concluded that the distribution of *P. laevis* reported in this study is typical of the distribution of *P. laevis* in trout from Ireland.

Kennedy *et al.* (1976) examined the sites occupied by *P. laevis* in the alimentary canal of seven different species of freshwater fish. Results for two fish species (goldfish, rainbow trout) were obtained from experimental infections. They demonstrated that the mean position of *P. laevis* along the intestine of brown trout was 14.5% (measured from the pyloric caeca to the anus), which corresponds to approximately 40% of the distance from the oesophagus to the anus (Kennedy, 1985). The authors also recorded a more anterior position for *P. laevis* in goldfish for higher intensity infections, which resulted from a wider anterior spread of the attachment region. The mean position decreased from 20.3% to 16.6% when the parasite burden was increased from 10 parasites per fish to 30 parasites per fish. A more anterior mean position for *P. laevis* in high intensity infections was also recorded in this study.

In a series of laboratory experiments Kennedy (1972a) examined the effects of temperature on the establishment and survival of *P. laevis* in goldfish. He demonstrated that the region of attachment of *P. laevis* was more anterior in starved fish, more posterior at lower temperatures, and that when crowded, the occupied region extended anteriorly. He also demonstrated that there was no movement of the *P. laevis* population, either up or down the alimentary tract during the course of the infection. Once worms attached at a particular site they remained there.

In the present study the mean position of *P. laevis* shifted anteriorly from April to November. This anterior shift in the mean position could be the result of increased summer temperatures in Lough Feeagh, or it could be consistent with the greater number of parasite individuals recorded in the summer months, and hence a crowding effect. It is likely that the number of parasite individuals recorded had some effect on the distribution of the population of *P. laevis* in the intestine of trout, as the mean position occupied was more anterior and the range of occurrence and niche width values were higher in high intensity infections.

The biggest difference between these two studies (Kennedy, 1972a; the present study) was the fact that the mean positions recorded by Kennedy (1972a) were substantially more anterior than the mean positions recorded in this study. This could be related to the fact that this study was carried out on wild trout, the preferred definitive host of *P. laevis* in Ireland, whereas the study by Kennedy (1972a) was an experimental study carried out on goldfish, an unsuitable host for *P. laevis*.

Kennedy (1984a) and Munro *et al.* (1989) examined the microhabitat utilisation of *P. laevis* in flounder. Both studies demonstrated that *P. laevis* occupied a posterior position along the intestine of flounder (in both studies most worms were found in the rectum), which was analogous to the results recorded for *P. laevis* recorded in brown trout. However, it is not possible to directly compare the intestinal distribution *P. laevis* in freshwater trout and marine flatfish. More recently Bates and Kennedy (1991a) demonstrated that *P. laevis* occupied posterior distributions in the intestine of experimental rainbow trout, with mean positions occurring around the 65-75% location. They also showed that the distribution of *P. laevis* did not change over time. The distributions recorded for *P. laevis* in experimental rainbow trout were comparable to the distributions of *P. laevis* in this study. However in an earlier study Kennedy *et al.* (1976) reported that the distribution of *P. laevis* in the intestine of experimental rainbow trout was substantially more posterior than its distribution in brown trout.

Thus, it appears that the microhabitat position occupied by *P. laevis* in brown trout in Ireland is somewhat more posterior than the position occupied by *P. laevis* in brown trout in England. However, the patterns of occurrence were similar, as in Ireland and England the mean position recorded for *P. laevis* became more anterior as the infection intensity increased. The differences in the mean position recorded for *P. laevis* between Ireland and England could be the result of stochastic processes, or they could be related to the fact that *P. laevis* exists as two distinct strains, an Irish strain which uses brown trout as its preferred definitive host (Kennedy *et al.*, 1978) and an English freshwater strain which uses chub and barbel as its preferred definitive hosts (Hine and Kennedy, 1974).

Q. Are the distributions of *P. laevis* in wild and stocked trout comparable?

When the distributions of *P. laevis* were compared between wild and stocked trout the mean position recorded for the total sample of *P. laevis* in wild trout (77.9%) was more posterior, and it also occurred over a greater range of the intestine (70.4%) than in stocked trout (mean position 70.5%; range 62%). When the distributions of *P. laevis* were compared between months, the mean positions recorded for wild trout were more posterior in May and November, and in all cases *P. laevis* occurred over a greater range of the intestine in wild trout. However the distribution of *P. laevis* in stocked trout in August may not have been typical for this month as only nine worms were recovered, compared to 62 in May, and 449 in November.

When the distribution of *P. laevis* was compared for low, medium and high intensity infections in wild and stocked trout, in all cases mean positions were more posterior in wild trout. Also, the range of occurrence along the intestine was smaller for stocked trout in medium and high intensity infections. However, niche width values were higher for stocked trout in low and medium intensity infections and identical to wild trout in high intensity infections.

Niche width values were calculated using Culver's 1972 standardised Shannon-Wiener function, H' . This index essentially describes the evenness of the distribution of a parasite in the intestine of its host. The function ranges from zero, where a parasite is present in only one section of the intestine to one, where the parasite is equally abundant in all sections of the intestine (Hair and Holmes, 1975). Thus the increased niche width values recorded in stocked trout can be explained by the fact that *P. laevis* was more abundant in more sections of the intestine than wild trout.

It is unclear why parasites in stocked trout should have slightly more anterior mean positions. Kennedy (1974a) suggested that temperature and crowding could affect the distribution of *P. laevis* in goldfish, similarly Kennedy *et al.* (1976) also reported a more anterior shift in the distribution with increased intensity of infection. It is unlikely the temperature could have caused such a difference in the mean attachment positions as both wild and stocked trout were exposed to the same natural temperature regimes in Lough Feeagh.

Similarly, it is unlikely that infection intensity is responsible, because in all months with the exception of November, substantially more *P. laevis* were found in wild trout, so if anything one would expect the mean position of *P. laevis* in stocked trout to be more posterior. Kennedy *et al.* (1976) concluded that the distribution of *P. laevis* in the alimentary canal of fish was primarily determined by the process of liberation, activation and establishment of the parasite and that it normally attaches in the first available space and remains there. It is conceivable that the microhabitat conditions in the intestine of stocked trout were more suitable, and as a result *P. laevis* was liberated sooner which resulted in suitable space for attachment occurring in a more anterior position, hence the more anterior mean positions recorded in stocked trout.

Q. Is the niche of *A. clavula* typical?

In Lough Feeagh *A. clavula* co-occurred with *P. laevis*, whereas in Clogher Lake *A. clavula* was the only species of acanthocephalan present, it was also one of the most dominant parasite species in the trout sample. Therefore, it is probably more appropriate to ask whether the niche of *A. clavula* when it co-occurred with another acanthocephalan species was comparable to the fundamental niche of *A. clavula* in brown trout, as recorded in Clogher Lake.

The mean position of the total sample of *A. clavula* in Lough Feeagh was approximately 60%. The minimum position, corresponding to the anterior pyloric caeca, was 29.15%, and the maximum position corresponding to the anus, was 100%. Thus, over 70% of the intestine was occupied by the parasite. A similar pattern was found when the total sample was examined by month (Table 5.19), a minimum of 52% of the intestine was occupied by the parasite in any one month. The mean positions recorded in each sample month became substantially more anterior from April to November and the niche width decreased from a peak in May and August to the lowest level in November. The mean position of *A. clavula* in low, medium and high intensity infections moved in an anterior direction as the infection intensity increased, however at each intensity level *A. clavula* occurred over a minimum of 68% of the length of the intestine. The niche width also decreased from low to high intensity infections.

The distribution of the total samples of *A. clavula* were comparable between Lough Feeagh and Clogher Lake (Table 5.19). When the samples were compared by month a similar overall pattern emerged, however in Lough Feeagh the mean position of *A. clavula* decreased substantially from April to November whereas in Clogher Lake there was only a slight decrease (Table 5.19). A similar pattern emerged when the distributions of *A. clavula* in low, medium and high intensity infections were compared between Lough Feeagh and Clogher Lake. In both cases the mean positions became more anterior from low to high intensity infections and in both cases the

interquartile range was substantially smaller in high intensity infections. It can be concluded that the same pattern of infection occurred for *A. clavula* in Clogher Lake and Lough Feeagh, and that *A. clavula* in Lough Feeagh also preferred the middle portion of the intestine of trout, but were capable of occurring all along the intestine.

Table 5.19 Comparison of the intestinal distributions of *A. clavula* in Lough Feeagh and Clogher Lake.

	April	May	August	November	Total
Clogher Lake					
Mean position (%)	61	61.3	59.6	55.6	59
Range (%)	71.7	65.2	68.3	67	71.7
Niche Width	0.8	0.8	0.8	0.8	0.8
Lough Feeagh					
Mean position (%)	76.6	67.5	53.7	47.1	59.7
Range (%)	52.7	61.5	69	61.8	70.9
Niche Width	0.7	0.8	0.8	0.6	0.9

The findings from Lough Feeagh agree with the findings of Conneely and McCarthy (1988) who examined the location of *A. clavula* in trout, and with the findings of Kennedy and Lord (1982) who examined the location of *A. clavula* in eels. In both studies *A. clavula* occupied an anterior position in the host intestine. The anterior shift in the mean position from April to November was also reported from Clogher Lake, but it was much more dramatic in Lough Feeagh. This anterior shift was also accompanied by a decrease in the interquartile range and niche width values. In contrast, Kennedy and Lord (1982) reported an anterior shift in the mean position of *A. clavula* with increasing infection intensity, but this anterior shift was accompanied by a corresponding increase in the niche width.

It appears that the situation in Lough Feeagh was analogous to the situation reported from Clogher Lake. Parasites probably bred in late spring or summer and were subsequently lost from their hosts, and followed by recruitment to the next generation (Kennedy and Moriarty, 1987). In Lough Feeagh and Clogher Lake some of the highest mean intensity values were recorded in November, which is consistent with an increase in recruitment. Kennedy and Lord (1982) suggested that *A. clavula* was

similar to *P. laevis* in respect of the fact that once it attached to the intestine it did not undergo posterior migration. They also suggested that similar to *P. laevis* the major determining process in site selection was the process of liberation and activation, and once these were complete the parasite would just establish itself in the first available site. These suggestions are consistent with the results reported from Lough Feeagh and Clogher Lake. They support the idea that the anterior shift in the mean position was as a result of parasite recruitment and the reduction in the niche width was as a result of older parasites being lost from the posterior portions of the intestine.

Q. Are the distributions of *A. clavula* in wild and stocked trout comparable?

Examination of the distribution of *A. clavula* in stocked trout suggests that it was generally comparable to the distribution of *A. clavula* in wild trout, although the mean position was more anterior and the niche width and range of occurrence values were slightly lower for stocked trout. However, when the distribution of *A. clavula* was compared between months a different pattern emerged. In wild trout the mean position became substantially more anterior, and the niche width and the interquartile range values decreased from April to November. Whereas, in stocked trout the mean position became more anterior in August, but then changed and became more posterior in November, similarly the niche width decreased from May to August and increased again in November.

When the distributions of *A. clavula* in low, medium and high intensity infections in wild trout were compared to those in stocked trout, all mean position values, ranges of occurrence and niche width values were lower in stocked trout. Thus, it can be concluded that the overall patterns of distribution of *A. clavula* in wild and stocked trout were comparable.

The anterior shift in the mean position recorded for *A. clavula* in stocked trout in August was probably related to the intensity of infection. The mean intensity values recorded for *A. clavula* in stocked trout in May and November were comparable, but

the value recorded for August was substantially higher. Kennedy and Lord (1982) recorded an anterior shift in the mean position of *A. clavula* in high intensity infections, but this shift was accompanied by an extension of the range. Similar to the situation recorded for *A. clavula* in wild trout the anterior shift as a result of increasing infection intensity was accompanied by a reduction in the niche width.

It is likely that a number of factors were operating together to which could account for the distribution of *A. clavula* in stocked trout. Firstly, as Kennedy and Moriarty (1987) proposed for *A. lucii* and *A. anguillae* it is likely that *A. clavula* bred in mid summer and worms were subsequently lost from the fish, although Chubb (1964) suggested that *A. clavula* did not exhibit a seasonal maturation cycle. Secondly, it is likely that new parasites were being recruited, and as suggested by Kennedy and Lord (1982), once liberated and activated, *A. clavula* was attaching at the first available site, resulting in an anterior distribution.

Thirdly as suggested for *P. laevis* it is possible that the microhabitat climate in the intestine of stocked trout was more favourable for attachment, which resulted in the mean position of *A. clavula* in the intestine of stocked trout being more anterior. Fourthly, it is likely that water temperatures in Lough Feeagh during the summer probably had some effect on the establishment of *A. clavula* in wild and stocked trout. Thus, it is probable that some, or all of the above-mentioned factors acted together to produce the distribution recorded for *A. clavula* in stocked trout.

Q. Is there any interaction between *P. laevis* and *A. clavula*?

A) Does the niche of *P. laevis* change in the presence of *A. clavula*?

When the distributions of *P. laevis* in low, medium and high intensity infections of *A. clavula* were compared to the distributions of *P. laevis* in low, medium and high intensity infections for the total sample, a number of patterns emerged. The mean position of *P. laevis* for the total sample became more anterior from low to high

intensity infections. The interquartile range, the range of occurrence and the niche widths were all highest in high intensity infections.

Therefore, it can be concluded that the distribution of *P. laevis* was extended in high intensity infections. When *P. laevis* co-occurred with *A. clavula* its mean position also became more anterior and the interquartile range increased from low to medium intensity infections. However, the niche width and the range of occurrence values decreased from low to medium intensity infections. Although the evidence suggests that the range of *P. laevis* decreased in the presence of *A. clavula*, it is likely that this was as a result of the reduced number of *P. laevis* individuals co-occurring with *A. clavula* in medium and high intensity infections, rather than any effect of *A. clavula*. For the total sample, 137 *P. laevis* occurred in medium intensity infections, and 795 occurred in high intensity infections, whereas, 15 *P. laevis* co-occurred with *A. clavula* in medium intensity infections and 4 co-occurred with *A. clavula* in high intensity infections. Therefore it appears that the presence of *A. clavula* had no significant effect on the distribution of *P. laevis*.

B) Does the niche of *A. clavula* change in the presence of *P. laevis*?

For *A. clavula* the mean position became more anterior from low to high intensity infections, but the range of occurrence remained constant. However, the niche width and interquartile range values decreased substantially from medium to high intensity infections. This suggests that although parasites were found all along the intestine (hence the constant range of occurrence) the majority of individuals were restricted to a much narrower area. When the distributions of *A. clavula* co-occurring with *P. laevis* were examined, mean positions, niche width values and range of occurrence values decreased from low to medium intensity infections and then increased in high intensity infections. No consistent pattern of increase or decrease was detectable.

The mean positions recorded for *A. clavula* in the presence of *P. laevis* were more posterior than those recorded for the total sample. Similar to the previous situation, this was probably due to the fact that substantially more *A. clavula* occurred in the

total sample in low, medium and high intensity infections than co-occurred with *P. laevis*. In the total sample 203 *A. clavula* occurred in low intensity infections, 324 occurred in medium intensity infections and 201 occurred in high intensity infections. This compares to 53 *A. clavula* co-occurring with *P. laevis* in low intensity infections and 16 *A. clavula* co-occurring with *P. laevis* in medium and high intensity infections. Thus it can be concluded that the presence of *P. laevis* had no significant effect on the distribution of *A. clavula*.

In a series of laboratory experiments Bates and Kennedy (1990, 1991b) examined the interactions between *P. laevis* and *A. anguillae* in experimental rainbow trout and then in their natural definitive hosts, chub and the European eel. In rainbow trout they demonstrated that in concurrent infections of the two species, the establishment and survival of *P. laevis* was unaffected by the presence of *A. anguillae*. However the presence of *P. laevis* at high intensities affected, not the establishment, but the survival of *A. anguillae*, and it required a number of weeks for this effect to become apparent. When similar experiments were repeated for *P. laevis* and *A. anguillae* in chub and eels, it was not possible to complete experiments in chub due to poor establishment and growth of parasites, and in eels there appeared to be no evidence of interspecific interactions either positive or negative.

The situation reported for *P. laevis* and *A. anguillae* in rainbow trout appears to be similar to the present study, although it was not possible to directly compare the two studies, as a different acanthocephalus species was compared to *P. laevis*, and rainbow trout were used as the final hosts. It is possible that the presence of *P. laevis* also reduced the survivorship of *A. clavula*, although it was not possible to examine this in the present study. The niche overlap values reported for *P. laevis* and *A. anguillae* (44.1%) were comparable to the niche overlap values reported for *P. laevis* and *A. clavula* in April and May in this study. In contrast, Kennedy (1985) reported that *A. clavula* could inhabit most of the intestine and that *P. laevis* had a more posterior distribution, yet when they occurred together the degree of overlap between the two species was low and they exhibited fairly clear site segregation.

Bates and Kennedy (1990) also demonstrated that in concurrent infections at high densities of *P. laevis* the position of *A. anguillae* was significantly altered so as to reduce the overlap with *P. laevis*. This effect was not reported from this study. The most likely reason for this is that the actual numbers of individuals which co-occurred was very small. For example only 16 *A. clavula* co-occurred with *P. laevis* in high intensity infections, compared to 201 *A. clavula* in high intensity infections in the total sample.

Kennedy *et al.* (1989) examined the distributions of *P. laevis* and *A. anguillae* and demonstrated that when they occurred in the same river system their distributions were discrete with little overlap, and where overlap did occur they were never found in the same fish. It is possible that some degree of host separation occurs between *P. laevis* and *A. clavula*. Although there was no evidence for competition between both species when their distributions along the intestine were examined, when the number of individuals co-occurring was examined, it could be seen that very few individuals of one species co-occurred with the other species at high intensity (Table 5.11; Table 5.13). The actual number of individuals of one species co-occurring with the other species was fewer than would be expected, which could suggest that some type of interaction was occurring, although the nature of such an interaction is unclear.

C) Does the same pattern occur in stocked trout?

The distribution of *P. laevis* in low, medium and high intensity infections of *A. clavula* in stocked trout was compared to the distribution of *P. laevis* in low, medium and high intensity infections in the total sample of stocked trout. The distribution of *P. laevis* was almost identical in low and medium intensity infections in stocked trout, niche width values, interquartile range values and mean position values were all comparable. For *P. laevis* co-occurring with *A. clavula* in stocked trout the niche width increased from low to medium intensity infections and the mean position became more anterior. However the differences in the distribution of *P. laevis* between low, medium and high intensity infections in the total sample of stocked trout and *P. laevis* co-occurring with *A. clavula* in low, medium and high intensity

infections were more likely to be related to the number of individuals co-occurring rather than any effects of *A. clavula*. Thus, the same conclusion can be drawn for stocked trout, as was drawn for wild trout, *A. clavula* does not appear to have any effect on the distribution of *P. laevis*.

The reverse situation was also examined for stocked trout, does the niche of *A. clavula* change in the presence of *P. laevis*. In the total sample of *A. clavula* all parameters decreased from low to high intensity infections. The mean position became more anterior and the interquartile range, the range of occurrence and the niche width decreased in value. Kennedy and Lord (1982) also recorded an anterior shift in the mean position with increasing infection intensity, however they also recorded an increase in the niche width. In this situation there was an anterior shift but worms appeared to more closely located around the mean value. For *A. clavula* co-occurring with *P. laevis* in stocked trout, the mean position became more anterior from low to high intensity infections, however the interquartile range, the range of occurrence and the niche width value all decreased from low to medium intensity infections and then increased in high intensity infections.

Again the same conclusions can be drawn for stocked trout as were drawn for wild trout. It is likely that the changes in the distribution of *A. clavula* in low, medium and high intensity infections of *P. laevis* are the results of chance and the low number of *A. clavula* co-occurring with *P. laevis*, rather than any effects of *P. laevis*. However as for wild trout it is possible that *P. laevis* has some negative effect on the survivorship of *A. clavula*, but this situation is impossible to test. Unfortunately it has not been possible to compare the results from this study with those of any other study on the actual or potential interactions between these two acanthocephalan species in wild or stocked fish as none exist.

Q. Is there any interaction between *P. laevis*, *A. clavula* and *E. crassum*?

A) Does the niche of *P. laevis* change in the presence of *E. crassum*?

The distribution of *P. laevis* when it co-occurred with *E. crassum* in low, medium and high intensity infections was compared to the distribution of *P. laevis* in low, medium and high intensity infections for the total sample. For the total sample, *P. laevis* followed the pattern reported by Kennedy *et al.* (1976), the range of occurrence, the niche width and the interquartile range increased as the infection intensity increased, and the mean position became more anterior. The distribution of *P. laevis* in low, medium and high intensity infections of *E. crassum* also followed a similar type pattern. The mean position was more anterior and the range of occurrence and the niche width values increased from low to high intensity infections. However the interquartile range decreased from low to medium intensity infections and increased in high intensity infections.

Although the distributions were similar between *P. laevis* in the total sample and *P. laevis* co-occurring with *E. crassum* when actual numbers were compared, the mean position of *P. laevis* when it co-occurred with *E. crassum* was more posterior than *P. laevis* in the total sample for all infection intensities. Similarly, the range of occurrence and the niche width values were smaller for *P. laevis* when it co-occurred with *E. crassum*. The niche overlap values for *P. laevis* and *E. crassum* were extremely small, the overlap value for the total sample was 0.01. Kennedy (1996a) reported that the preferred location of *E. crassum* was the pyloric caeca and Kennedy (1985) reported that *P. laevis* occupied a more posterior position of the intestine. Niche overlap values from this study support these suggestions. Kennedy (1985) also suggested that because of their preferred locations there would be little overlap between the *E. crassum* and *P. laevis*, this appears to be the cases, but does this mean that there could be no interaction between the two species?

In this study it appears that the niche of *P. laevis* was restricted in the presence of *E. crassum*. The same conclusion was drawn for *A. clavula* and *E. crassum* in Clogher

Lake. The presence of *E. crassum* appeared to reduce the realised niche of *A. clavula*. These findings contrast with those of Chappell (1969) and Grey and Hayunga (1980) who also studied the interactions between cestodes and acanthocephalans and reported that in all cases the acanthocephalan displaced the cestode. To explain how *P. laevis* affected the survivorship of *A. anguillae*, Bates and Kennedy (1990) introduced the idea that an exclusion zone or 'zone sanitaire' surrounded *P. laevis* in which the survival of *A. anguillae* was reduced. A similar idea could be used to explain the apparent reduction in the realised niche of *P. laevis* in the presence of *E. crassum*, when both species occupied opposite ends of the intestine and there was very little overlap between them.

In contrast, in a later paper Bates and Kennedy (1991b) examined the potential interaction between *A. anguillae* and *P. laevis* in eels, they could find no evidence for a 'zone sanitaire' or exclusion zone surrounding either parasite species. However, it is possible that the reduced niche width and more posterior positions recorded for *P. laevis* in the presence of *E. crassum* were as a result of the fewer numbers of *P. laevis* found, rather than any negative effects of *E. crassum*.

B) Does the niche of *A. clavula* change in the presence of *E. crassum*?

The mean position of *A. clavula* for the total sample became more anterior from low to high intensity infections, and the interquartile range and the niche width also decreased from low to high intensity infections. Thus, the distribution of *A. clavula* was reduced in high intensity infections in the total sample. When *A. clavula* occurred with *E. crassum* the mean position was also more anterior in high intensity infections, however the niche width values and the range of occurrence increased from low to high intensity infections of *E. crassum*. The situation reported for *A. clavula* in the presence of *E. crassum* was comparable to the situation reported by Kennedy and Lord (1982), as the infection intensity increased the mean position became more anterior and the niche width and range of occurrence increased.

However when the values were compared between *A. clavula* in the total sample and *A. clavula* co-occurring with *E. crassum*, in all cases mean position values were more posterior for *A. clavula* when it co-occurred with *E. crassum*. Similarly, the range of occurrence was lower in all cases for *A. clavula* when it co-occurred with *E. crassum*, and the niche widths were substantially lower for *A. clavula* in low and medium intensity infections of *E. crassum*. These differences probably resulted from the fact that very few *A. clavula* co-occurred with *E. crassum* in low and medium intensity infections.

Thus it appears that *E. crassum* did not adversely affect the distribution of *A. clavula* in Lough Feeagh. In contrast, in Clogher Lake the presence of *E. crassum* appeared to substantially reduce the realised niche of *A. clavula*. Kennedy and Lord (1982) reported that site specificity was low for *A. clavula*, because although it had a preferred location, it could occur all along the intestine. Niche overlap values for *A. clavula* and *E. crassum* varied from 1 to 0.15, and thus support the idea that site fidelity in *A. clavula* was low. A total of 234 *A. clavula* co-occurred with *E. crassum* in Clogher Lake, whereas, in Lough Feeagh a total of 81 *A. clavula* co-occurred with *E. crassum*. Thus, it is possible that the lack of interaction between *A. clavula* and *E. crassum* in Lough Feeagh resulted from the fact that not enough *A. clavula* co-occurred with *E. crassum* to compensate for the lack of site specificity of *A. clavula* and thus make a reduction in its realised niche apparent, i.e. there was too much noise in the system to make any patterns recognisable.

C) Does the same pattern occur in stocked trout?

The distribution of *P. laevis* in low, medium and high intensity infections of *E. crassum* in stocked trout followed a similar pattern to *P. laevis* in low, medium and high intensity infections in the total sample. In both cases the mean position was more anterior in high intensity infections, and in both cases the range of occurrence and the niche width values were highest in high intensity infections. However, similar to the situation with *P. laevis* and *E. crassum* in wild trout, when the actual values were compared a number of differences appeared. In all cases the distribution of *P. laevis*

when it co-occurred with *E. crassum* was more posterior than the distribution of *P. laevis* in the total sample. The most anterior distribution for *P. laevis* when it co-occurs with *E. crassum* did not overlap with the most posterior position recorded for *P. laevis* for the total sample. Similarly, the niche widths and range of occurrence values were substantially smaller for *P. laevis* when it co-occurred with *E. crassum* than for *P. laevis* in the total sample. Thus the same conclusion can be drawn for stocked trout as was drawn for wild trout, namely, that the niche of *P. laevis* was restricted in the presence of *E. crassum*.

The distributions of *A. clavula* in low, medium and high intensity infections of *E. crassum* in stocked trout were also examined. The same situation was recorded for *A. clavula* co-occurring with *E. crassum* in stocked trout as was recorded for *A. clavula* co-occurring with *E. crassum* in wild trout. The mean position became more anterior from low to high intensity infections, and the range of occurrence and niche width values increased. In contrast, for the total sample of *A. clavula* in stocked trout the niche width and the range of occurrence were lower in high intensity infections.

When the mean position values were compared between the total sample of *A. clavula* in stocked trout and *A. clavula* co-occurring with *E. crassum*, in all cases the mean position recorded for *A. clavula* co-occurring with *E. crassum* was more posterior. Thus, the same conclusions can be drawn for *A. clavula* co-occurring with *E. crassum* in low, medium and high intensity infections in stocked trout as were drawn for wild trout. Again, it has not been possible to compare the results from this study with those of any other study on the potential interactions between *A. clavula* and *E. crassum* in stocked trout, or between an acanthocephalan and a cestode in any stocked fish, as none exist.

Chapter 6

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6.1 Organisation of chapter six

In chapter six the population biology of *P. laevis* is discussed. The chapter is divided into four sections. In section one a brief summary of the component community parameters of *P. laevis* in wild and stocked trout is presented. The size of *P. laevis* was then examined for the total trout sample and for the trout samples from each month. The total sample of *P. laevis* was then divided into low, medium and high intensity infections and the size of worms was examined at each category of intensity. The size of *P. laevis* was then compared between wild and stocked trout for the total sample and for each sample month. In the last part of this section the *P. laevis* samples in wild and stocked trout were divided into low, medium and high intensity infections and the size of worms were compared between wild and stocked trout at each category of intensity.

In section two the size of female *P. laevis* were examined for the total trout sample and for the trout samples from each month. The total sample of female *P. laevis* was then divided into low, medium and high intensity infections and the size of worms was examined at each category of intensity. Finally the size of female *P. laevis* was compared between wild and stocked trout for the total sample and for each sample month.

In section three the proportion of female *P. laevis* that were defined as stage I, II or III maturity was described for the total sample and for wild and stocked trout. The size of worms in each maturity stage was examined for each sample month. The size of stage I, II and III female *P. laevis* was then examined in low, medium and high intensity infections. In the final part of this section the size of stage I, II and III female *P. laevis* was compared between wild and stocked trout.

In chapter five the niches of the total sample of *P. laevis* were examined for each sample month and in low, medium and high intensity infections. In this section the niches of female *P. laevis* were examined for the total sample and for each sample

month. The niches of female *P. laevis* were then examined in low, medium and high intensity infections. In the final part of section four, the niches of stage I, II and III female *P. laevis* were examined for the total sample and for each sample month. The niches of stage I, II and III female *P. laevis* were then examined in low, medium and high intensity infections.

6.2 Summary of the component community parameters of *P. laevis*

The component community parameters of *P. laevis* have been summarised for each monthly sample and for the total sample of wild (Table 6.1) and stocked trout (Table 6.2). The component community parameters of *P. laevis* have previously been discussed in detail in Chapter four. However, they have been included here to refresh the reader and to reiterate the main component community parameters of *P. laevis*, when its population biology was being discussed.

6.3 Examination of the size of *P. laevis* in wild and stocked trout in Lough Feeagh

6.3.1 Examination of the size of *P. laevis* in the total trout sample and in each sample month

Length

The mean length of *P. laevis* for the total sample was 8.48mm(± 2.78) (Table 6.3; Fig 6.1). Mean length values increased from April to a peak in August and subsequently decreased in November (Table 6.3; Fig 6.1).

Weight

The mean weight of *P. laevis* recorded for the total sample was 4.58mg(± 5.1) (Table 6.3; Fig 6.2). Mean weight values decreased from April to May, increased to the highest value in August and subsequently decreased to the lowest level in November (Table 6.3; Fig 6.2).

One-way analysis of variance (ANOVA) showed significant differences in the lengths of *P. laevis* between months for the overall sample (F ratio = 178.2; df = 3,1716; $p \leq 0.0001$). Least squares difference post hoc tests showed significant differences in the length of *P. laevis* between November and April ($p \leq 0.0001$), November and August ($p \leq 0.0001$), August and April ($p \leq 0.0001$), August and May ($p \leq 0.0001$) and April

and May ($p \leq 0.009$). There was no significant difference in the length of *P. laevis* between November and May.

A similar analysis was performed for the weights of *P. laevis* ($\log(x+1)$ transformed). One-way analysis of variance (ANOVA) showed significant differences in the weights of *P. laevis* between months for the overall sample (F ratio = 220.4; $df = 3,1713$; $p \leq 0.0001$). Least squares difference post hoc tests showed significant differences in *P. laevis* weight between November and every other month ($p \leq 0.0001$ in every case), and between August and every other month ($p \leq 0.0001$ in every case). There was no significant difference in the $\log(x+1)$ transformed weight of *P. laevis* between April and May.

6.3.2 Examination of the size of the total sample of *P. laevis* in low, medium and high intensity infections

The total sample of *P. laevis* was divided into low, medium and high intensity infections and the lengths and weights of worms in each intensity category were examined. The same criteria were used to define low, medium and high intensity infections as were used when the niches of *P. laevis* were being examined in Chapter five. Thus a low intensity infection of *P. laevis* was one to five worms, a medium intensity infection of *P. laevis* was six to nine worms and a high intensity infection was ten or more worms.

Length

The mean length of worms decreased from 9.3mm(± 3.28) in low intensity infections to 7.89mm(± 2.44) in medium and 8.32mm(± 2.58) in high intensity infections (Table 6.4; Fig 6.3).

Weight

The mean weights of *P. laevis* decreased substantially from 6.98mg(± 7.47) in low intensity infections to 3.62mg(± 3.48) in medium and 3.92mg(± 3.94) in high intensity infections (Table 6.4, Fig 6.3).

One-way analysis of variance (ANOVA) was used to compare the lengths and weights of the total sample of *P. laevis* between low, medium and high intensity infections. The lengths of *P. laevis* in the total sample were shown to be significantly different between low, medium and high intensity infections (F ratio = 25.1; df = 2,1717; $p \leq 0.0001$). Least squares difference post hoc tests showed significant differences in the lengths of *P. laevis* between medium and low and high and low intensity infections ($p \leq 0.0001$ in both cases) and also between high and medium intensity infections ($p = 0.03$).

One-way analysis of variance (ANOVA) also showed significant differences in the log (x+1) transformed weights of *P. laevis* between low, medium and high intensity infections (F ratio = 61.2; df = 2,1714; $p \leq 0.0001$). Least squares difference post hoc tests showed significant differences in the log (x+1) transformed weight of *P. laevis* between low and medium and low and high intensity infections ($p \leq 0.0001$ in both cases).

Table 6.1 Summary of the component community data for *P. laevis* in wild trout in 1997 and 1998.

	April	May	August	November	Total
No. of fish examined	60	64	88	45	257
% Prevalence	48.3	90.6	73.9	46.7	67.3
Mean Abundance ($\pm$ S.D.)	1.87(3.9)	9.05(11.8)	4.14(5.9)	3.73(7.9)	4.76(8.2)
Mean Intensity ($\pm$ S.D.)	3.86(4.9)	9.98(12)	5.60(6.2)	8(10.2)	7.1(9.1)
Range	0 – 24	0 – 80	0 – 29	0 – 40	0 – 80
S ² / X	8.24	15.32	8.39	16.91	14.11

Table 6.2 Summary of the component community data for *P. laevis* in stocked trout in 1997 and 1998.

	May	August	November	Total
No. of fish examined	47	25	50	122
% Prevalence	34.0	20	84	51.6
Mean Abundance ($\pm$ S.D.)	1.15(2.5)	0.36(0.9)	9.46(12)	4.39(8.9)
Mean Intensity ($\pm$ S.D.)	3.38(3.3)	1.80(0.1)	11.26(12.3)	8.51(10.9)
Range	0 – 12	0 – 4	0 – 56	0 – 56
S ² / X	5.3	2.29	15.25	17.97

Table 6.3 Statistics summarising the length distributions (in mm) and weight distributions (in mg) of *P. laevis* in trout from Lough Feeagh for the total sample (wild and stocked trout) and for each sample month.

	April	May	August	November	Total
Length					
Count	263	488	339	630	1720
Mean ($\pm$ S.D.)	7.31(2.19)	7.79(2.41)	11.17(2.95)	8.06(2.21)	8.48(2.78)
Minimum	2	1	2	3	1
Maximum	14	16	21	20	21
Range	12	15	19	17	20
Weight					
Count	263	488	337	629	1717
Mean ($\pm$ S.D.)	4.01(3.13)	3.74(2.85)	9.16(6.94)	3.02(4.52)	4.58(5.1)
Minimum	1	0.5	1	***	***
Maximum	20	39	51	40	51
Range	19	38.5	50	40	51

*** = The minimum weight was smaller than the lowest value recorded by the balance.

Table 6.4 Statistics summarising the length and weight distributions (in mm and mg respectively) of *P. laevis* in low, medium and high intensity infections in the total trout sample (wild and stocked trout) from Lough Feeagh.

	Low		Medium		High	
	Length	Weight	Length	Weight	Length	Weight
Count	396	395	240	240	1084	1082
Mean ($\pm$ S.D.)	9.3(3.28)	6.98(7.47)	7.89(2.44)	3.62(3.48)	8.32(2.58)	3.92(3.94)
Minimum	3	0.5	2	0.5	1	***
Maximum	21	51	16	24	19	38
Range	18	49.5	14	23.5	18	38

*** = The minimum weight was smaller than the lowest value recorded by the balance.

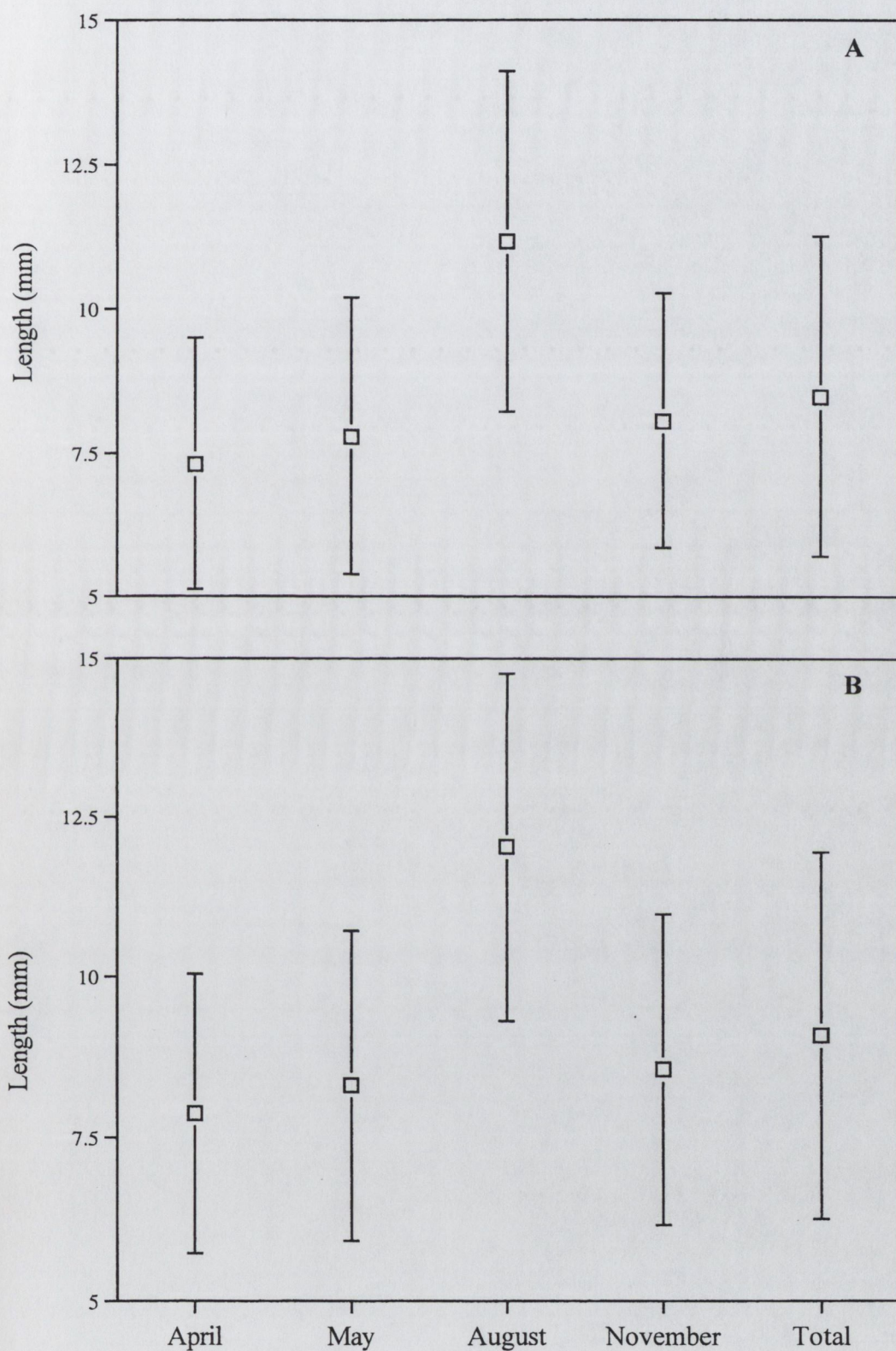


Fig 6.1 Mean lengths ($\pm$ S.D.) of *P. laevis* in each sample month and for the total sample, for worms of both sexes (A), female worms (B).

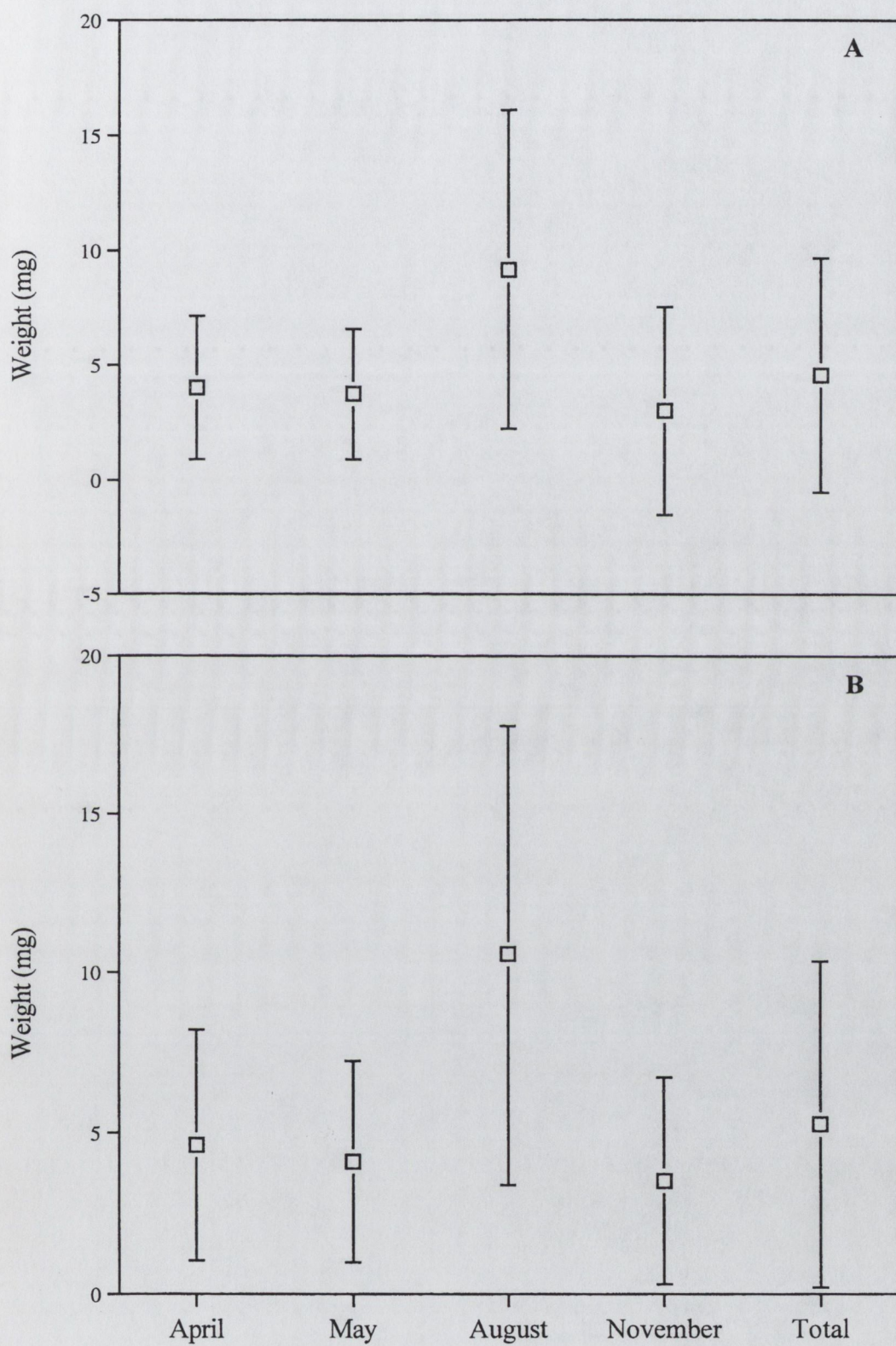


Fig 6.2 Mean weights ($\pm$ S.D.) of *P. laevis* in each sample month and for the total sample, for worms of both sexes (A), female worms (B).

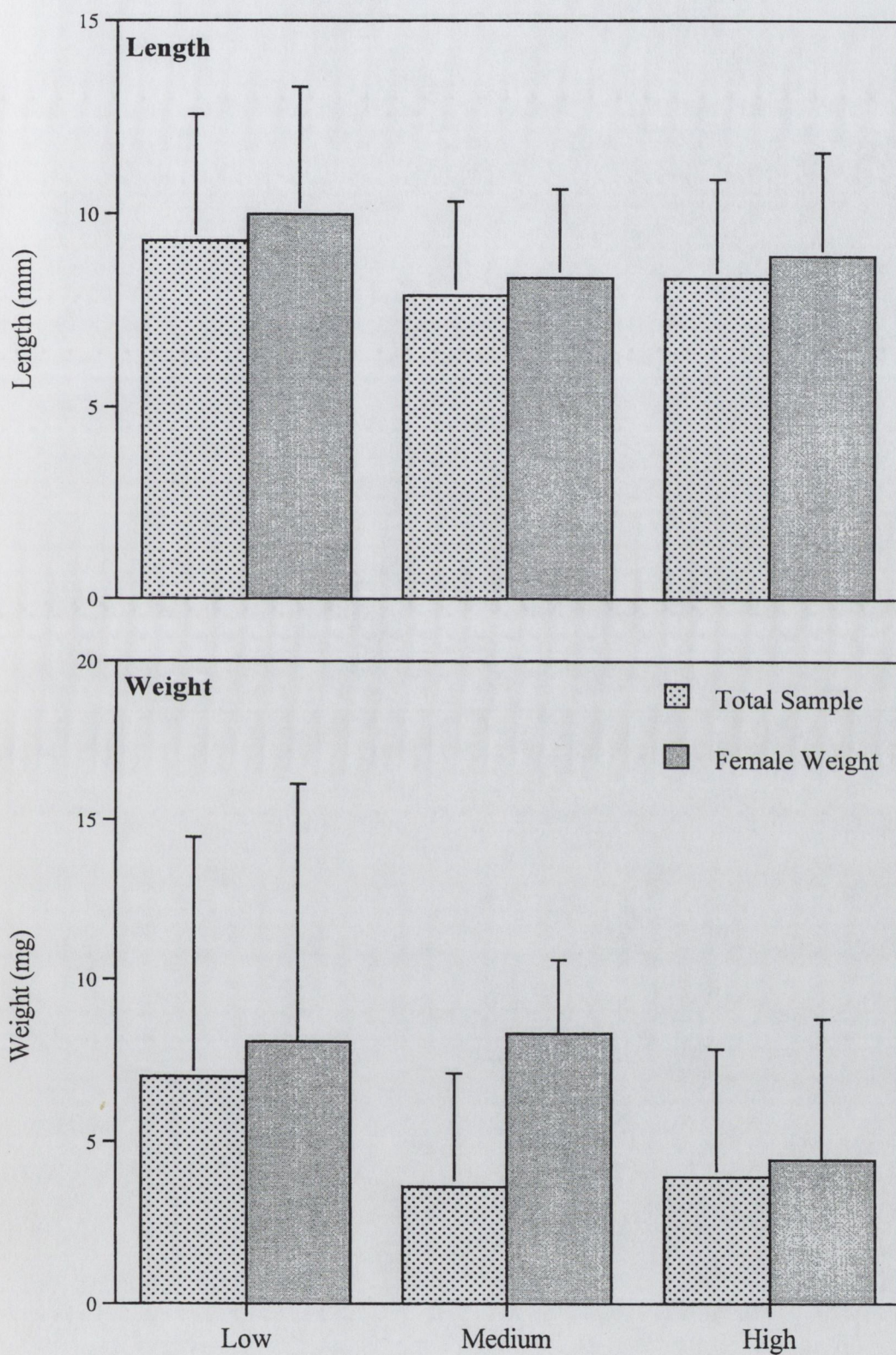


Fig 6.3 Mean lengths and weights (+ S.D.) for the total sample and total female sample of *P. laevis* in low, medium and high intensity infections in trout from Lough Feeagh.

6.3.3 Comparison of the size of *P. laevis* between months for the total sample for wild and stocked trout

In this section the meristic data related to the population biology of *P. laevis* was compared between wild and stocked trout. In all cases a set of statistics summarising the distribution of lengths and weights of *P. laevis* have been provided.

Length

The mean length recorded for *P. laevis* was 8.76mm(± 3.02) for the total sample of wild trout and 7.83mm(± 1.96) for the total sample of stocked trout (Fig 6.4). In wild trout mean lengths increased from April to August and decreased in November (Table 6.5). In stocked trout mean length values decreased from April to May, peaked in August and decreased again in November (Table 6.6).

Weight

Mean weights were 5.49mg(± 5.66) for the total sample of wild trout and 2.44mg(± 2.29) for the total sample of stocked trout (Fig 6.5). The mean weights of wild trout increased from April to a peak in August (Table 6.5), whereas the mean weights of stocked trout decreased from April to May and increased to a peak in August and decreased again in November (Table 6.6; Fig 6.5).

Two-way analysis of variance was used to examine the relationship between month, fish host status (whether worms were present in wild or stocked trout) and the length of *P. laevis* worms present. A significant difference existed in the length of *P. laevis* recorded in each month (F ratio = 5.1; $df = 3,1712$; $p \leq 0.002$). No significant differences existed in the lengths of *P. laevis* recorded between wild and stocked trout, however the interaction between the month and host status was significant (F ratio = 36.9; $df = 3,1712$; $p \leq 0.0001$).

Two-way analysis of variance was also used to examine the relationship between month, host status (whether worms were present in wild or stocked trout) and the log ($x+1$) transformed weights of *P. laevis* worms present. A significant difference

existed in the weight of *P. laevis* recorded in each month (F ratio = 33.0; df = 3,1708; $p \leq 0.0001$). No significant differences existed in the weights of *P. laevis* recorded between wild and stocked trout. However, the interaction between the month and the host status was significant (F ratio = 42.3; df = 3,1708; $p \leq 0.001$).

6.3.4 Comparison of the size of *P. laevis* in low, medium and high intensity infections in wild and stocked trout

In this section the total sample of *P. laevis* in wild and stocked trout was divided into low, medium and high intensity infections and the distributions of the lengths and weights of *P. laevis* were then compared between them.

Length

The mean length for *P. laevis* in low intensity infections was 9.5mm(± 3.4) in wild trout and 8.41mm(± 2.25) for stocked trout. Similarly the mean length for *P. laevis* in medium intensity infections was 8.09mm(± 2.7) in wild trout and 7.59mm(± 1.9) in stocked trout and for high intensity infections the mean length was 8.57mm(± 2.8) in wild trout and 7.76mm(± 1.9) for stocked trout (Fig 6.6). Thus the mean length of *P. laevis* was higher for wild trout in all cases. The mean length value of *P. laevis* in wild and stocked trout decreased from low to medium intensity infections and increased again in high intensity infections (Table 6.7; Table 6.8).

Weight

The mean weight for *P. laevis* in low intensity infections was 7.72mg(± 8) for wild trout and 3.8mg(± 3) for stocked trout. For medium intensity infections the mean weight was 4.33mg(± 3.9) for wild trout and 2.55mg(± 2.4) for stocked trout and for high intensity infections the mean weight was 4.76mg(± 4.3) for wild trout and 2.11mg(± 1.9) for stocked trout (Fig 6.7). In all cases the mean weight of *P. laevis* was higher for wild trout. In wild trout mean weight values for *P. laevis* decreased from low to medium intensity infections and increased again in high intensity infections. In

stocked trout mean weight values for *P. laevis* decreased from low to high intensity infections (Table 6.7; Table 6.8).

Two-way analysis of variance was used to examine the relationship between infection intensity (low, medium or high), fish host status (whether worms were present in wild or stocked trout) and the length of *P. laevis* worms present. A significant difference existed in the length of *P. laevis* recorded in low, medium and high intensity infections (F ratio = 11.3; df = 2,1714; $p \leq 0.0001$). Significant differences existed in the lengths of *P. laevis* recorded between wild and stocked trout (F ratio = 20.4; df = 1,1714; $p \leq 0.0001$), however the interaction between infection intensity and host status was not significant.

Two-way analysis of variance was also used to examine the relationship between infection intensity (low, medium, high), host status (whether worms were present in wild or stocked trout) and the log (x+1) transformed weights of *P. laevis* worms present. A significant difference existed in the weight of *P. laevis* recorded in low, medium and high intensity infections (F ratio = 34.8; df = 2,1710; $p \leq 0.0001$). Significant differences existed in the weights of *P. laevis* recorded between wild and stocked trout (F ratio = 154.3; df = 1,1710; $p \leq 0.0001$). The interaction between infection intensity and the host status was also significant (F ratio = 3.2; df = 2,1710; $p = 0.04$).

Table 6.5 Statistics summarising the length distributions (in mm) and weight distributions (in mg) of *P. laevis* in wild trout from Lough Feeagh for the total sample and for each sample month.

	April	May	August	November	Total
Length					
Count	229	450	336	192	1207
Mean ($\pm$ S.D.)	6.89(1.80)	7.75(2.4)	11.18(2.95)	9.15(2.82)	8.76(3.02)
Minimum	2	2	2	3	2
Maximum	13	16	21	20	21
Range	11	14	19	17	19
Weight					
Count	229	450	334	192	1205
Mean ($\pm$ S.D.)	3.54(2.57)	3.71(2.91)	9.16(6.97)	5.6(7.35)	5.49(5.66)
Minimum	1	0.5	1	***	***
Maximum	20	39	51	40	51
Range	19	38.5	50	40	51

*** = The minimum weight was smaller than the lowest value recorded by the balance.

Table 6.6 Statistics summarising the length distributions (in mm) and weight distributions (in mg) of *P. laevis* in stocked trout from Lough Feeagh for the total sample and for each sample month.

	April	May	August	November	Total
Length					
Count	34	38	3	438	513
Mean ($\pm$ S.D.)	10.15(2.49)	8.37(2.56)	10.33(3.51)	7.58(1.69)	7.83(1.96)
Minimum	5	1	7	3	1
Maximum	14	12	14	13	14
Range	9	11	7	10	13
Weight					
Count	34	38	3	437	512
Mean ($\pm$ S.D.)	7.18(4.5)	4.03(1.99)	9(5.29)	1.89(1.25)	2.44(2.29)
Minimum	1	1	5	0.5	0.5
Maximum	16	8	15	12	16
Range	15	7	10	11.5	15.5

Table 6.7 Statistics summarising the length and weight distributions (in mm and mg respectively) of *P. laevis* low, medium and high intensity infections in wild trout from Lough Feeagh.

	Low	Medium	High
Length			
Count	321	144	742
Mean ($\pm$ S.D.)	9.5(3.4)	8.09(2.7)	8.57(2.8)
Minimum	3	2	2
Maximum	21	16	19
Range	18	14	17
Weight			
Count	320	144	741
Mean ($\pm$ S.D.)	7.72(8)	4.33(3.9)	4.76(4.3)
Minimum	0.5	0.5	***
Maximum	51	24	38
Range	50.5	23.5	38

*** = The minimum weight was smaller than the lowest value recorded by the balance.

Table 6.8 Statistics summarising the length and weight distributions (in mm and mg respectively) of *P. laevis* in low, medium and high intensity infections in stocked trout from Lough Feeagh.

	Low	Medium	High
Length			
Count	75	96	342
Mean ($\pm$ S.D.)	8.41(2.25)	7.59(1.9)	7.76(1.9)
Minimum	4	3	1
Maximum	14	13	14
Range	10	10	13
Weight			
Count	75	96	341
Mean ($\pm$ S.D.)	3.8(3)	2.55(2.4)	2.11(1.9)
Minimum	1	0.5	0.5
Maximum	15	15	16
Range	14	14.5	15.5

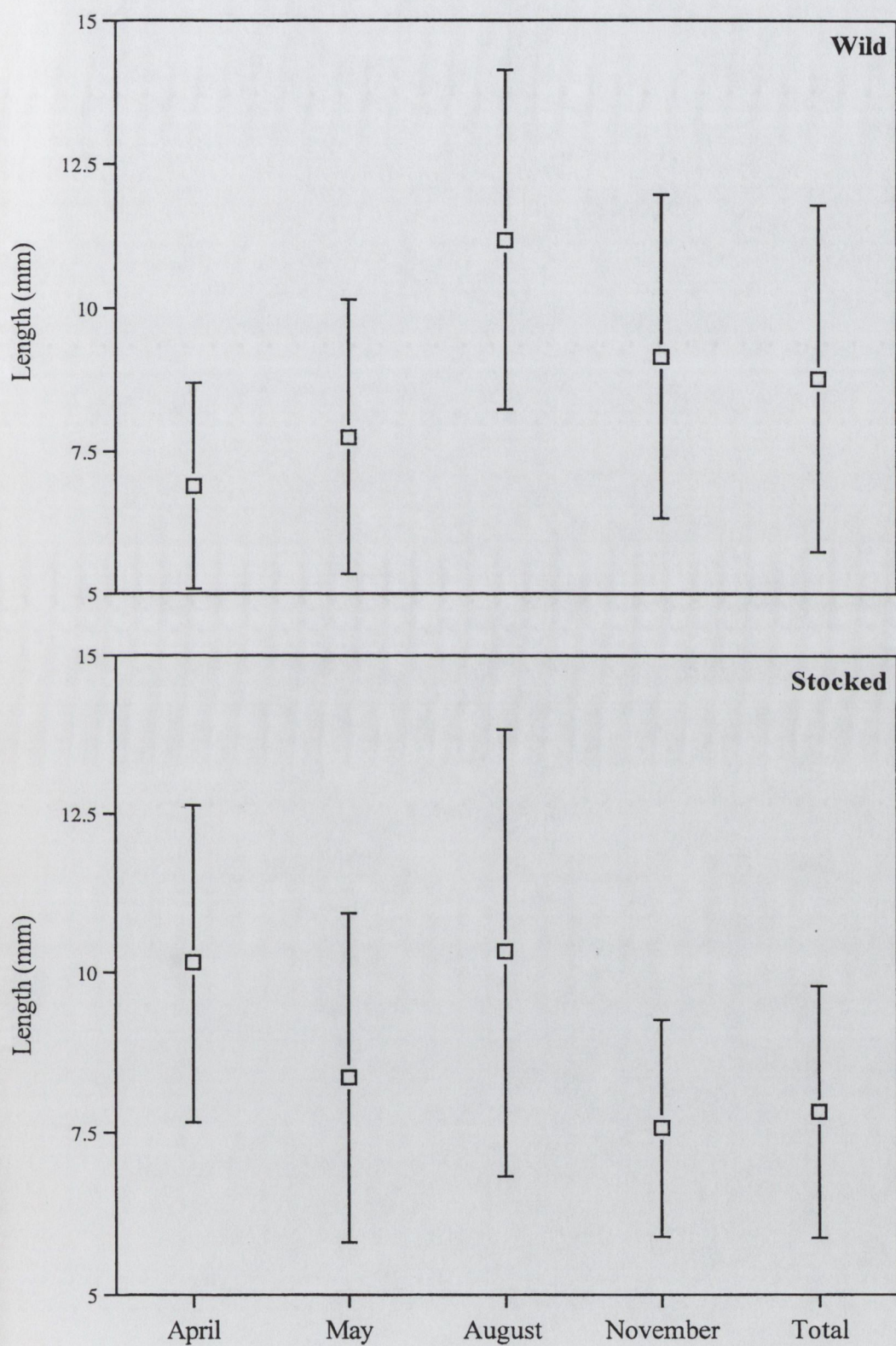


Fig 6.4 Mean lengths (+/- S.D.) of *P. laevis* in each sample month and for the total sample of wild and stocked trout.

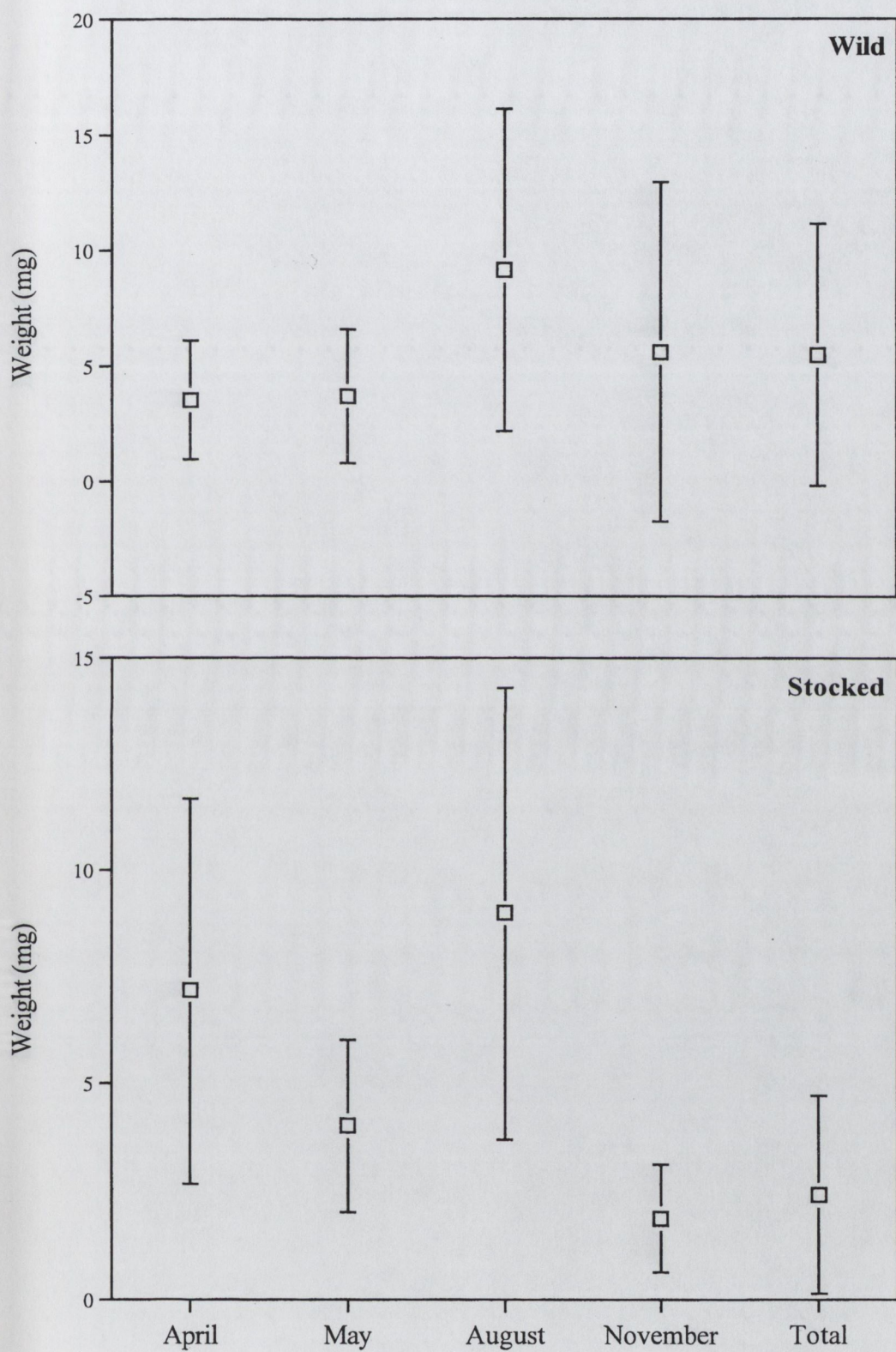


Fig 6.5 Mean weights (+/- S.D.) of *P. laevis* in each sample month and for the total sample of wild and stocked trout.

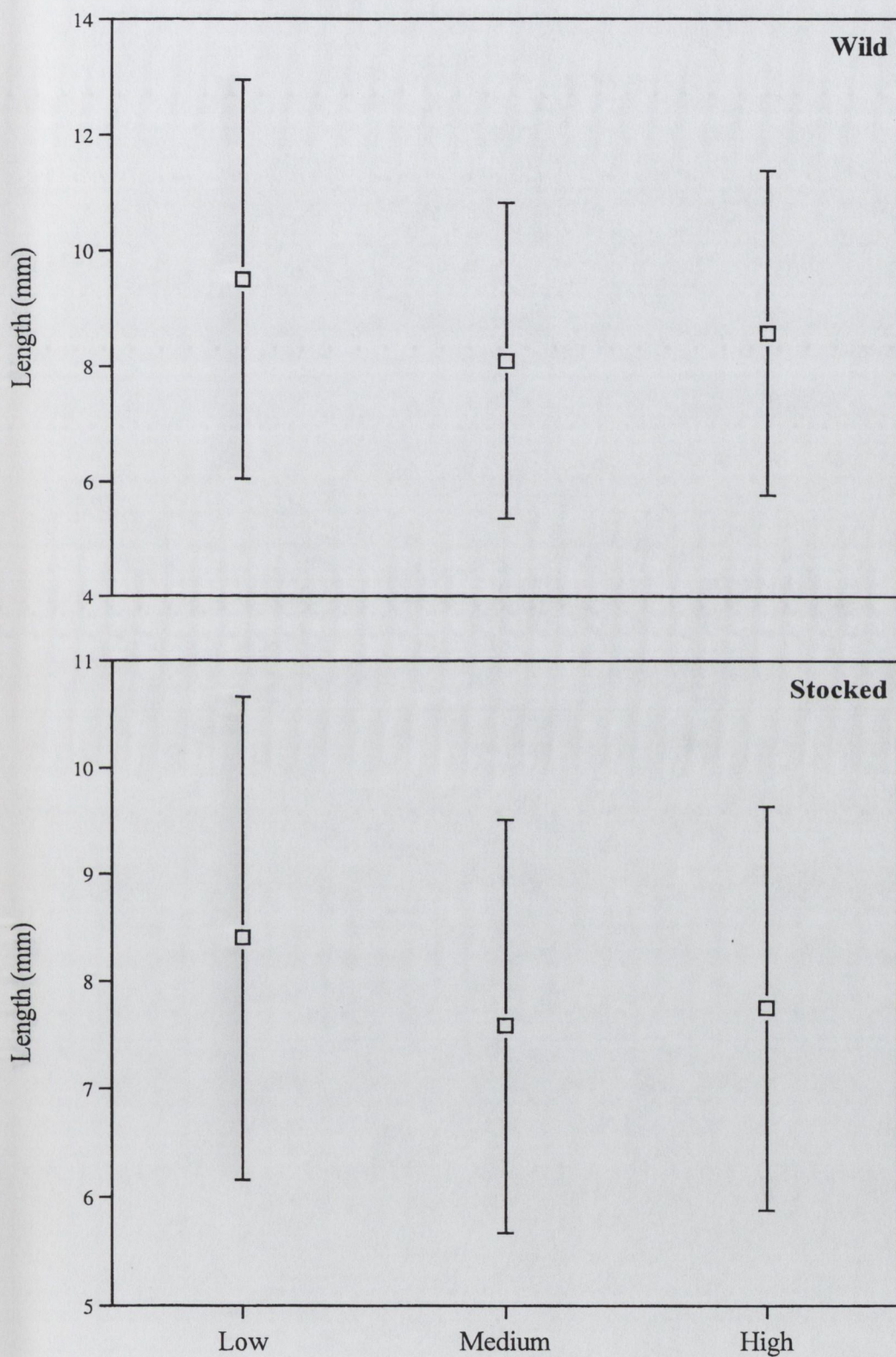


Fig 6.6 Mean lengths ($\pm$ S.D.) of *P. laevis* in low, medium and high intensity infections in wild and stocked trout.

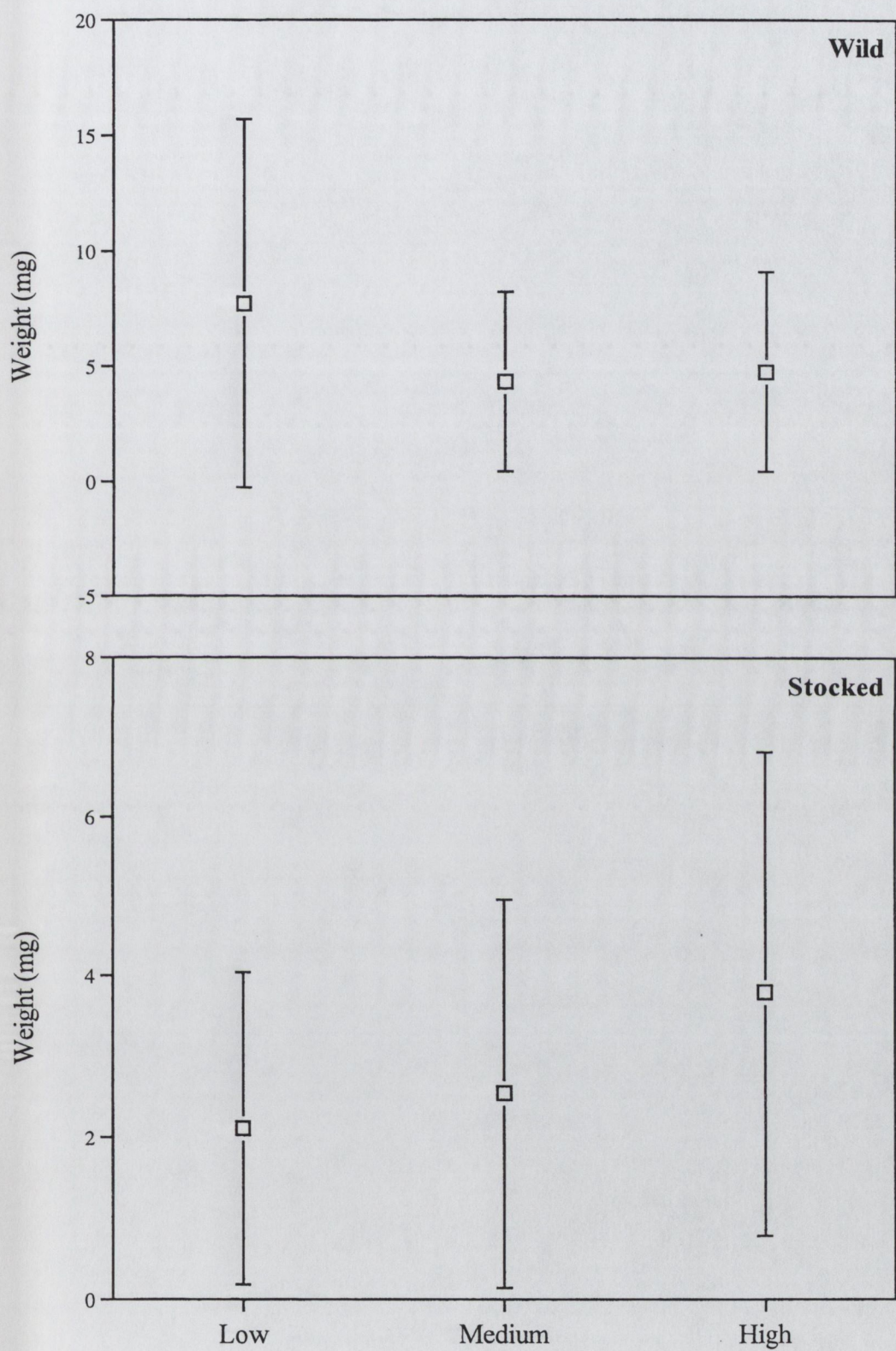


Fig 6.7 Mean weights ($\pm$ S.D.) of *P. laevis* in low, medium and high intensity infections in wild and stocked trout.

6.4 Examination of the size of female *P. laevis* in wild and stocked trout in Lough Feeagh

6.4.1 Examination of the size of female *P. laevis* in the total sample and each sample month

Length

The mean length value recorded for the total sample of female *P. laevis* was 9.1mm(± 2.85) (Table 6.9). The mean length of female *P. laevis* increased from April to a peak in August and decreased slightly in November. The mean length value recorded for the total sample of female *P. laevis* was comparable to the value recorded in November (Table 6.9)

Weight

The mean weight value recorded for the total sample of *P. laevis* was 5.29mg(± 5.68) (Table 6.9). The mean weight of female *P. laevis* decreased from April to May, peaked in August and decreased to its lowest level in November (Table 6.9; Fig 6.2).

One-way analysis of variance showed significant differences in the lengths of female *P. laevis* between months for the overall sample (F ratio = 108.6; df = 3,854; $p \leq 0.001$). Least squares difference post hoc tests showed significant differences in the lengths of female *P. laevis* between August and every other month ($p \leq 0.0001$ in every case) and between April and November ($p \leq 0.003$).

One-way analysis of variance also showed significant differences in the log (x+1) transformed weights of female *P. laevis* between sample months (F ratio = 122.6; df = 3,854; $p \leq 0.0001$). Least squares differences post hoc tests showed significant differences in the log (x+1) transformed weights of female *P. laevis* between November and every other month ($p \leq 0.0001$ in every case) and August and every other month ($p \leq 0.0001$ in every case).

6.4.2 Examination of the size of the female sample of *P. laevis* in low, medium and high intensity infections

Length

In a similar manner to the previous section the lengths and weights of female *P. laevis* were examined in low, medium and high intensity infections. Mean length values decreased from 9.99mm(± 3.3) in low intensity infections to 8.34mm(± 2.29) in medium intensity infections and increased to 8.9mm(± 2.69) in high intensity infections (Table 6.10; Fig 6.3).

Weight

Mean weight values decreased from 8.06mg(± 8.07) in low intensity infections to 4.02mg(± 3.8) in medium intensity infections and increased to 4.45mg(± 4.34) in high intensity infections (Table 6.10; Fig 6.3).

One-way analysis of variance showed significant differences in the lengths of female *P. laevis* between low, medium and high intensity infections (F ratio = 16.3; df = 2,855; $p \leq 0.0001$). Least squares difference post hoc tests showed significant differences in the lengths of female *P. laevis* between low and medium and low and high intensity infections ($p \leq 0.0001$ in both cases).

One-way analysis of variance showed significant differences in the log (x+1) transformed weights of female *P. laevis* between low, medium and high intensity infections (F ratio = 38.5; df = 2,855; $p \leq 0.0001$). Least squares difference post hoc tests showed significant differences in the weights (log (x+1) transformed) of female *P. laevis* between low and medium and low and high intensity infections ($p \leq 0.0001$ in both cases).

Table 6.9 Statistics summarising the length distributions (in mm) and weight distributions (in mg) of female *P. laevis* in trout from Lough Feeagh for the total sample and for each sample month.

	April	May	August	November	Total
Length					
Count	146	232	173	307	858
Mean ($\pm$ S.D.)	7.88(2.16)	8.32(2.4)	12.04(2.72)	8.57(2.41)	9.1(2.85)
Minimum	3	3	2	3	2
Maximum	14	16	20	20	20
Range	11	13	18	17	18
Weight					
Count	146	232	173	307	858
Mean ($\pm$ S.D.)	4.62(3.58)	4.11(3.12)	10.59(7.21)	3.52(5.22)	5.29(5.68)
Minimum	1	0.5	1	***	***
Maximum	20	39	41	40	41
Range	19	38.5	40	40	41

*** = The minimum weight was smaller than the lowest value recorded by the balance.

Table 6.10 Statistics summarising the length and weight distributions (in mm and mg respectively) of female *P. laevis* in low, medium and high intensity infections in the total trout sample from Lough Feeagh.

	Low		Medium		High	
	Length	Weight	Length	Weight	Length	Weight
Count	213	213	116	116	529	529
Mean ($\pm$ S.D.)	9.99(3.3)	8.06(8.07)	8.34(2.29)	4.02(3.8)	8.9(2.69)	4.45(4.34)
Minimum	3	1	2	0.5	3	***
Maximum	20	41	16	24	19	31
Range	17	40	14	23.5	16	31

*** = The minimum weight was smaller than the lowest value recorded by the balance.

6.4.3 Comparison of the size of female *P. laevis* in between stocked and wild trout in the total sample and in each sample month

Length

The mean length of female *P. laevis* for the total sample was 8.52mm(± 2.95) for wild trout and 7.89mm(± 1.99) for stocked trout (Table 6.11; Table 6.12). Mean length values for wild trout increased from April to a peak in August and decreased again in November (Table 6.11; Fig 6.8). In stocked trout mean length values decreased from April to November (Table 6.12; Fig 6.9).

Weight

The mean weight of female *P. laevis* was 5.27mg(± 5.28) for the total sample of wild trout and 2.48mg(± 2.35) for the total sample of stocked trout (Table 6.11; Table 6.12). Mean weights of female *P. laevis* in wild trout increased from April to August and decreased in November (Table 6.11; Fig 6.8). Mean weights of female *P. laevis* in stocked trout decreased from April to November (Table 6.12; Fig 6.9).

Two-way analysis of variance was used to examine the relationship between month, fish host status (whether worms were present in wild or stocked trout) and the length of female *P. laevis* worms present. A significant difference existed in the length of *P. laevis* recorded in each month (F ratio = 4.0; df = 3,850; $p \leq 0.007$). No significant differences existed in the lengths of *P. laevis* recorded between wild and stocked trout, however the interaction between month and host status was significant (F ratio = 23.2; df = 3,850; $p \leq 0.0001$).

Two-way analysis of variance was also used to examine the relationship between month, fish host status (whether worms were present in wild or stocked trout) and the log (x+1) transformed weights of female *P. laevis* worms present. Significant differences existed in the weights of female *P. laevis* recorded in each month (F ratio = 20.9; df = 3,849; $p \leq 0.0001$). No significant differences existed in the weights of *P. laevis* recorded between wild and stocked trout. However, the interaction between month and the host status was significant (F ratio = 25.3; df = 3,849; $p \leq 0.0001$).

Table 6.11 Statistics summarising the length distributions (in mm) and weight distributions (in mg) of female *P. laevis* in wild trout from Lough Feeagh for the total sample and for each sample month.

	April	May	August	November	Total
Length					
Count	155	233	187	87	662
Mean (± S.D.)	6.76(1.86)	7.48(2.09)	10.86(3.04)	9.41(2.8)	8.52(2.95)
Minimum	2	3	2	4	2
Maximum	13	15	18	18	18
Range	11	12	16	14	16
Weight					
Count	155	233	186	87	661
Mean (± S.D.)	3.44(2.53)	3.46(2.29)	8.52(6.29)	6.43(8.02)	5.27(5.28)
Minimum	1	0.5	1	0.5	0.5
Maximum	20	20	39	40	40
Range	19	19.5	38	39.5	39.5

Table 6.12 Statistics summarising the length distributions (in mm) and weight distributions (in mg) of female *P. laevis* in stocked trout from Lough Feeagh for the total sample and for each sample month.

	April	May	August	November	Total
Length					
Count	30	24	2	314	370
Mean (± S.D.)	10.07(2.59)	8(2.73)	8.5(2.12)	7.67(1.72)	7.89(1.99)
Minimum	5	1	7	3	1
Maximum	14	12	10	13	14
Range	9	11	3	10	13
Weight					
Count	30	24	2	314	370
Mean (± S.D.)	7.1(4.7)	3.83(1.97)	6(1.41)	1.92(1.27)	2.48(2.35)
Minimum	1	1	5	0.5	0.5
Maximum	16	8	7	12	16
Range	15	7	2	11.5	15.5

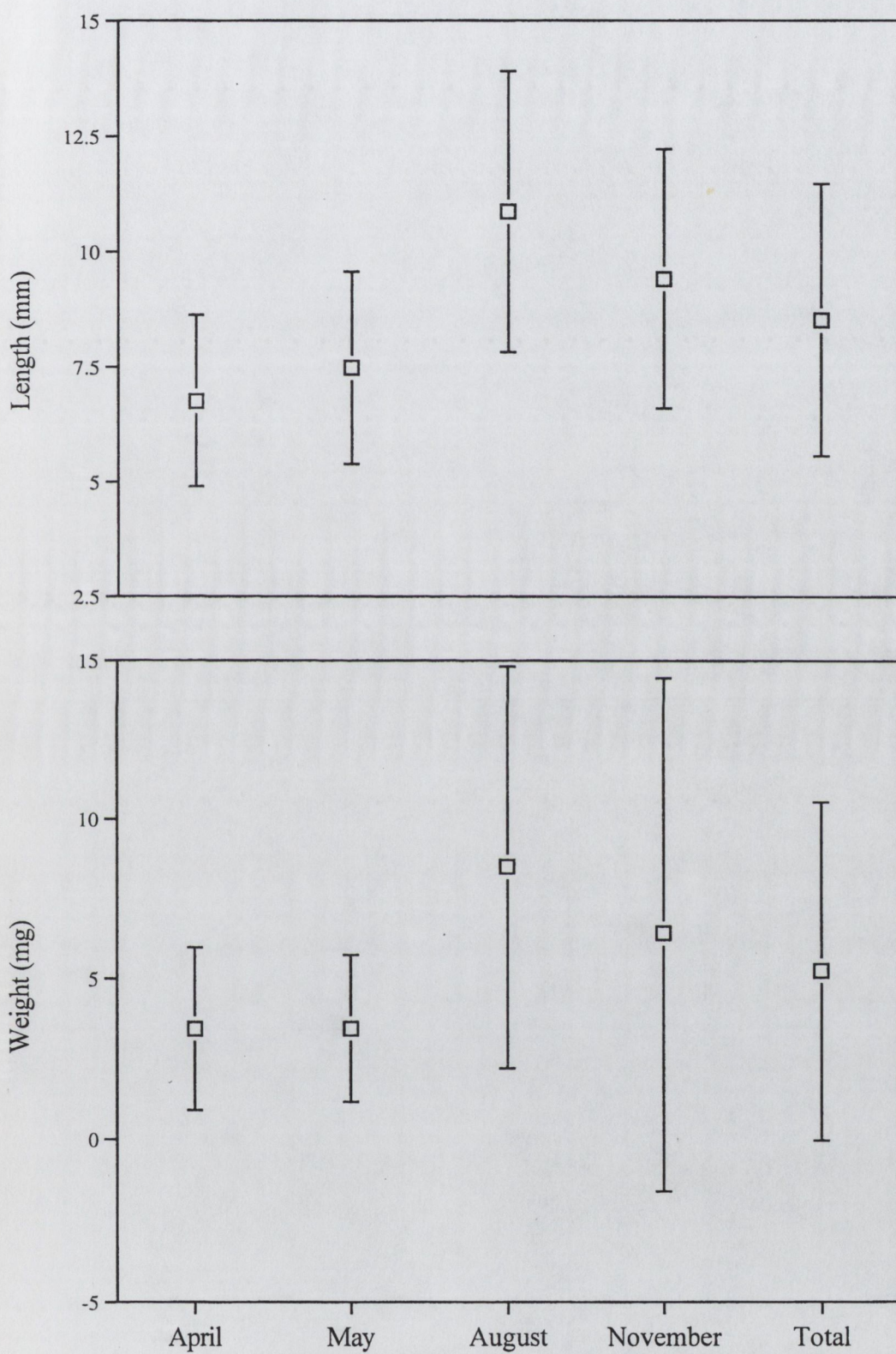


Fig 6.8 Mean lengths and weights ($\pm$ S.D.) of female *P. laevis* in wild trout for each sample month and for the total sample.

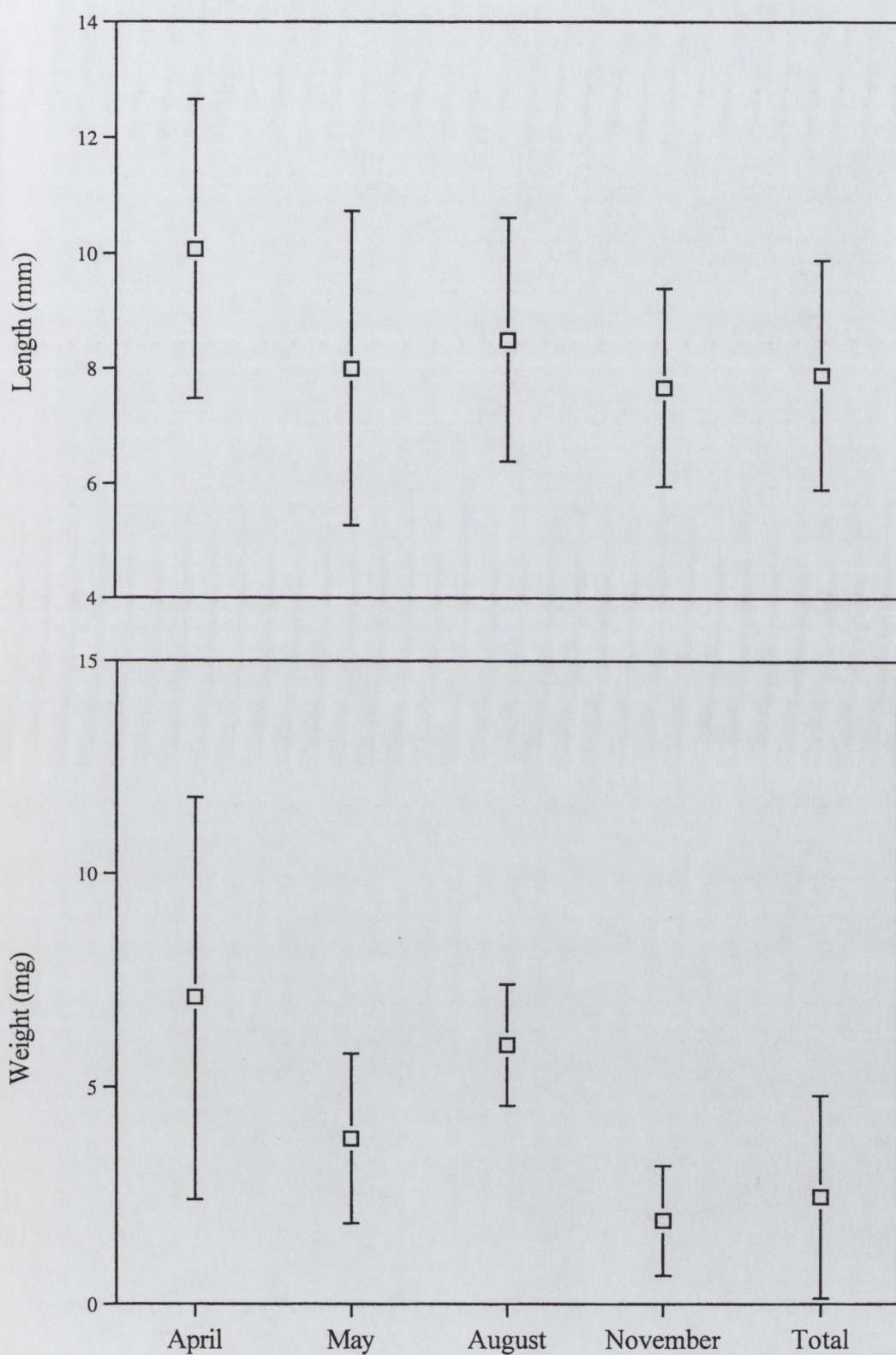


Fig 6.9 Mean lengths and weights ($\pm$ S.D.) of female *P. laevis* in stocked trout for each sample month and for the total sample.

6.5 Examination of the size of stage I, II and III female *P. laevis* in Lough Feeagh

6.5.1 Examination of the size of female *P. laevis* in stage I, II and III maturity in the total trout sample and in each sample month

In this section the maturity status of 742 female *P. laevis* was assessed. The maturity status of females was classed as being either stage I, II or III. The lengths and weights of female *P. laevis* were examined in each maturity stage and then compared between maturity stages. 65% of the total sample of *P. laevis* were of stage I maturity, 15% of the sample were of stage II maturity and the remaining 20% were of stage III maturity (Table 6.13). 52% of the total sample of *P. laevis* occurring wild trout were of stage I maturity, 20% were of stage II maturity and 2%8 were of stage III maturity (Table 6.14). For stocked trout 98% of the *P. laevis* sample were of stage I maturity, 2% were of stage II maturity and no *P. laevis* of stage III maturity were recorded (Table 6.15). Actual numbers and percentage totals were also given for each sample month (Table 6.13-6.15).

Chi-squared tables were used to examine the relationship between maturity status of female *P. laevis* (whether worms were of stage I or II maturity) and the fish host status (whether fish were wild or stocked) (Table 6.16). Only stage I and II female *P. laevis* were included in this analysis, as the main underlying assumption of chi-squared tables, that the value of any individual cell should not fall below five, was violated. No stage III female *P. laevis* were found in stocked trout. Percentage of column totals showed that similar proportions of stage I female *P. laevis* were found in wild and stocked trout, whereas significantly more stage II female *P. laevis* were found in wild trout than stocked trout (Chi-square = 64.73; $p \leq 0.0001$) (Table 6.16).

Stage I, II and III length

The mean length for the total sample of female worms was 8.1mm(± 2.36) for stage I female *P. laevis*, 8.36mm(± 2.14) for stage II female *P. laevis* and 12.01mm(± 2.71) for stage III female *P. laevis* (Table 6.17; Fig 6.10). For stage I female *P. laevis* mean lengths decreased from April to May, increased to a peak in August and subsequently

decreased in November. The mean length values for stage II female *P. laevis* increased consistently from April to August, and decreased in November. Mean length values for stage III female *P. laevis* increased from their lowest level in April, to a peak in November (Table 6.17; Fig 6.10).

Stage I, II and III weight

The mean weight for the total sample of female worms was 3.48mg(± 3.69) for stage I female *P. laevis*, 4.43mg(± 2.86) for stage II female *P. laevis* and 11.11mg(± 8.33) for stage III female *P. laevis* (Table 6.18; Fig 6.11). Mean weight values for stage I female *P. laevis* decreased from April to May, peaked in August and decreased to their lowest level in November. Mean weight values for stage II female *P. laevis* decreased from April to May, peaked in August and subsequently decreased to their lowest level in November. For stage III female *P. laevis* mean weight values decreased from April to May, increased in August and peaked in November (Table 6.18; Fig 6.11).

Two-way analysis of variance was used to examine the relationship between month, maturity status (whether female *P. laevis* were stage I, II or III) and the length of female *P. laevis* worms present. A significant difference existed in the length of *P. laevis* recorded in each month (F ratio = 33.9; df = 3,730; $p \leq 0.0001$). Significant differences existed in the lengths of *P. laevis* recorded between stage I, II and III females (F ratio = 52.2; df = 2,730; $p \leq 0.0001$) and the interaction between month and maturity status was also significant (F ratio = 10.0; df = 6,730; $p \leq 0.0001$).

Two-way analysis of variance was also used to examine the relationship between month, maturity status (whether female *P. laevis* were stage I, II or III) and the log (x+1) transformed weights of female *P. laevis* worms present. A significant difference existed in the weight of *P. laevis* recorded in each month (F ratio = 14.1; df = 3,729; $p \leq 0.0001$). Significant differences existed in the weights of female *P. laevis* recorded between stage I, II and III females (F ratio = 53.2; df = 2,729; $p \leq 0.0001$).

Table 6.13 Summary of the numbers and percentages of the total sample of stage I, II and III female *P. laevis* in trout from Lough Feeagh for the total sample and for each sample month.

	April	May	August	November	Total
Stage I					
Count	91	101	23	266	481
% of Total	62%	56%	17%	95%	65%
Stage II					
Count	46	55	10	2	113
% of Total	32%	31%	7%	0.7%	15%
Stage III					
Count	9	23	104	12	148
% of Total	6%	13%	76%	4.3%	20%
Total					
Count	146	179	137	280	742
% of Total	100%	100%	100%	100%	100%

Table 6.14 Summary of the number and percentage of the total sample of stage I, II and III female *P. laevis* in wild trout from Lough Feeagh for the total sample and for each sample month.

	April	May	August	November	Total
Stage I					
Count	77	84	20	87	268
% of Total	61%	52%	15%	87%	52%
Stage II					
Count	41	55	9	1	106
% of Total	32%	34%	7%	1%	20%
Stage III					
Count	9	23	102	12	146
% of Total	7%	14%	78%	12%	28%
Total					
Count	127	162	131	100	520
% of Total	100%	100%	100%	100%	100%

Table 6.15 Summary of the number and percentage of the total sample of stage I, II and III female *P. laevis* in stocked trout from Lough Feeagh for the total sample and for each sample month.

	April	May	August	November	Total
Stage I					
Count	16	20	3	178	217
% of Total	80%	100%	100%	99%	98%
Stage II					
Count	4	0	0	1	5
% of Total	20%	0%	0%	1%	2%
Stage III					
Count	0	0	0	0	0
% of Total	0%	0%	0%	0%	0%
Total					
Count	20	20	3	179	222
% of Total	100%	100%	100%	100%	100%

Table 6.16 Contingency table comparing the proportions of stage I and II female *P. laevis* in wild and stocked trout in Lough Feeagh.

Row Totals = Wild or Stocked Trout

Column Totals = Maturity Status

	Stage I		Stage II	Total
Wild	264	Wild	108	372
	71		29	100
	54.9		95.6	62.6
	44.4		18.2	62.6
Stocked	217	Stocked	5	222
	97.7		2.25	100
	45.1		4.42	37.4
	36.5		0.84	37.4
Total	481	Total	113	594
	81		19	100
	100		100	100
	81		19	100

Count

% of Row Total

% of Column Total

% of Table Total

Chi - square = 64.73; df = 1; p < 0.0001

Table 6.17 Statistics summarising the length distributions (in mm) of stage I, II and III female *P. laevis* in wild and stocked trout from Lough Feeagh for the total sample and for each sample month.

	April	May	August	November	Total
Stage I					
Count	91	101	23	266	481
Mean (± S.D.)	7.88(2.15)	7.18(2.19)	11(4.07)	8.28(1.98)	8.1(2.36)
Minimum	3	2	2	3	2
Maximum	14	20	20	13	20
Range	11	18	18	10	18
Stage II					
Count	46	55	10	2	113
Mean (± S.D.)	7.78(1.7)	8.23(1.94)	11.2(2.66)	11(2.93)	8.36(2.14)
Minimum	4	4	6	9	4
Maximum	13	13	15	13	15
Range	9	9	9	4	11
Stage III					
Count	9	23	104	12	148
Mean (± S.D.)	9.11(1.83)	10.26(2.87)	12.27(2.22)	15.33(2.71)	12.01(2.71)
Minimum	6	5	6	11	5
Maximum	12	16	18	20	20
Range	6	11	12	9	15

Table 6.18 Statistics summarising the weight distributions (in mg) of stage I, II and III female *P. laevis* in wild and stocked trout from Lough Feeagh for the total sample and for each sample month.

	April	May	August	November	Total
Stage I					
Count	91	101	23	266	481
Mean (± S.D.)	4.62(3.58)	3.18(1.75)	10.83(10.5)	2.61(2.04)	3.48(3.69)
Minimum	1	0.5	1	***	***
Maximum	20	9	41	15	41
Range	19	8.5	40	15	41
Stage II					
Count	46	55	10	2	113
Mean (± S.D.)	4.38(3.15)	3.91(1.68)	7.7(4.6)	3.35(1.63)	4.43(2.86)
Minimum	1	1.5	1	2.5	1
Maximum	16	9	16	4.5	16
Range	15	7.5	15	2	15
Stage III					
Count	9	23	104	12	148
Mean (± S.D.)	7(4.84)	6.87(7.39)	10.8(6.64)	25(11.21)	11.11(8.33)
Minimum	2	1	2	8	1
Maximum	18	39	39	40	40
Range	16	38	37	32	39

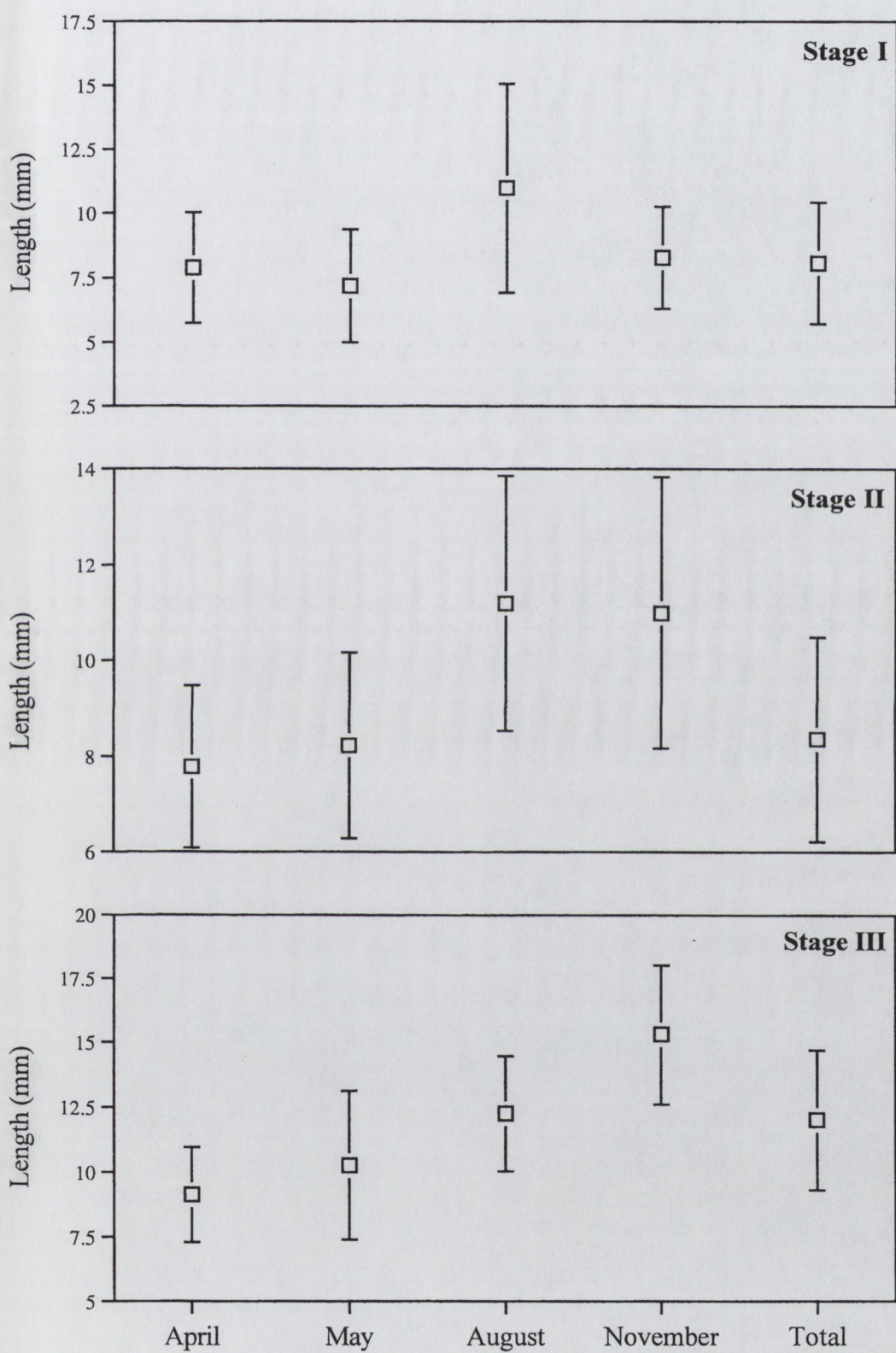


Fig 6.10 Mean lengths ($\pm$ S.D.) of female *P. laevis* at stage I, II and III maturity in each sample month and for the total sample.

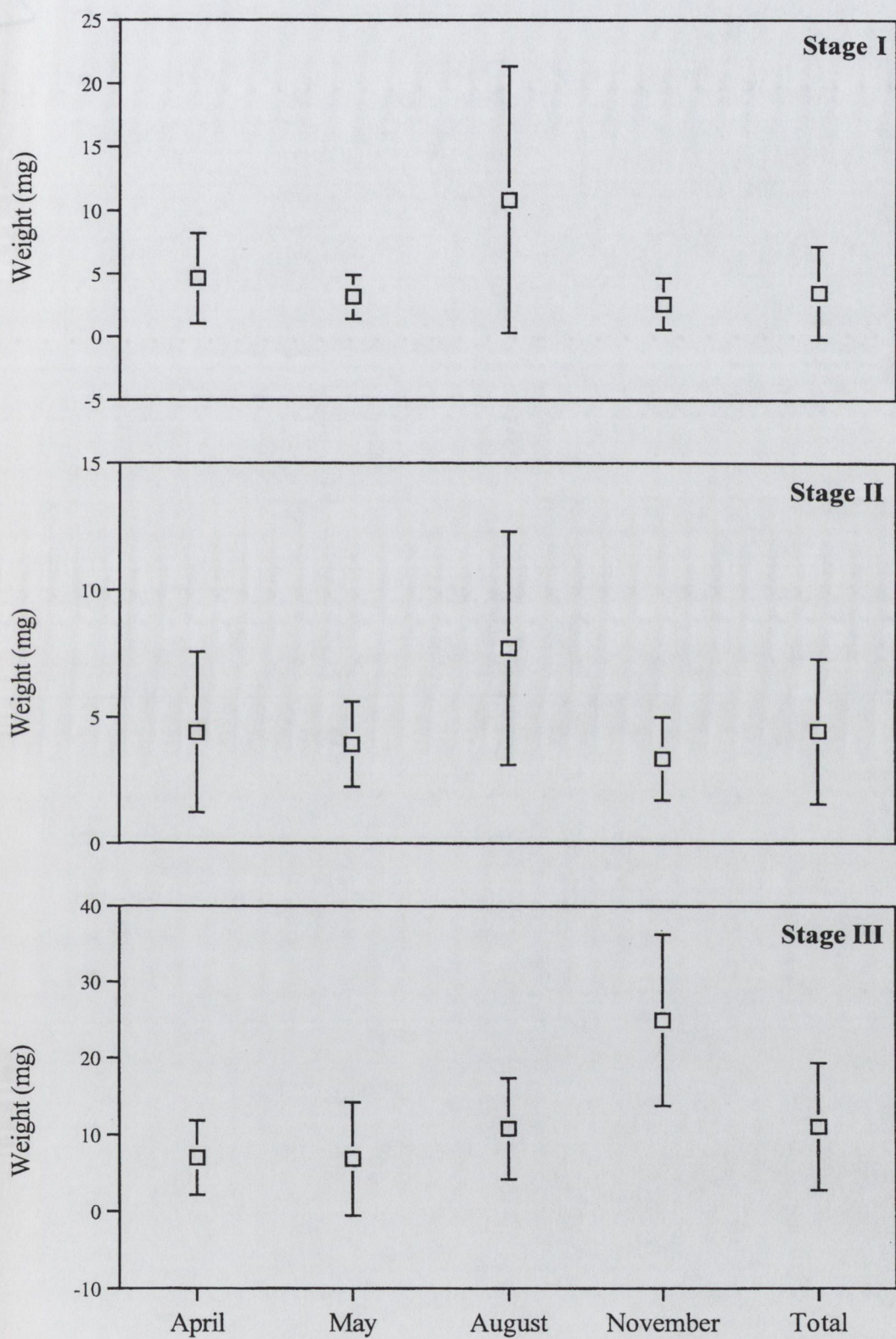


Fig 6.11 Mean weights ($\pm$ S.D.) of female *P. laevis* at stage I, II and III maturity in each sample month and for the total sample.

and the interaction between month and maturity status was also significant (F ratio = 13.4; df = 6,729; $p \leq 0.0001$).

6.5.2 Examination of the size of stage I, II and III female *P. laevis* in low, medium and high intensity infections

In this section the total female sample was separated by maturity status, into stage I, II or III female *P. laevis*, and the lengths and weights of worms in each maturity stage were examined in low, medium and high intensity infections.

Stage I length and weight

The mean length of stage I female *P. laevis* decreased from 8.72mm(± 2.93) in low intensity infections to 7.79mm(± 2.11) in medium intensity infections and increased slightly to 7.97mm(± 2.17) in high intensity infections (Table 6.19; Fig 6.12). Mean weight values decreased consistently from 5.46mg(± 5.99) in low intensity infections to 2.83mg(± 2.45) in high intensity infections (Table 6.19; Fig 6.13).

Stage II length and weight

The mean length of stage II female *P. laevis* decreased from 8.21mm(± 2.24) in low intensity infections to 8mm(± 1.54) in medium intensity infections and subsequently increased to 8.46mm(± 2.2) in high intensity infections (Table 6.20; Fig 6.12). Mean weight values decreased consistently from 5.23mg(± 3.75) in low intensity infections to 4.5mg(± 2.27) in medium intensity infections and 4.16mg(± 2.61) in high intensity infections (Table 6.20; Fig 6.13).

Stage III length and weight

The mean lengths of stage III female *P. laevis* decreased from 12.77mm(± 13.1) in low intensity infections to 10.66mm(± 1.45) in medium intensity infections and increased to 11.81mm(± 2.56) in high intensity infections (Table 6.21; Fig 6.12). The mean weight values for stage III female *P. laevis* decreased substantially from 15.49mg(± 11.1) in low intensity infections to 7.25mg(± 5.73) in medium intensity

infections, and then increased to 9.45mg($\pm$ 5.88) in high intensity infections (Table 6.21; Fig 6.13).

Two-way analysis of variance was used to examine the relationship between maturity status (whether female *P. laevis* were stage I, II or III), infection intensity (low, medium or high intensity infections) and the length of female *P. laevis* worms present. A significant difference existed in the length of *P. laevis* recorded between stage I, II and III females (F ratio = 73.5; df = 2,733; $p \leq 0.0001$). A significant difference existed in the lengths of female *P. laevis* recorded in low, medium and high intensity infections (F ratio = 4.0; df = 2,733; $p = 0.02$), however the interaction between maturity status and infection intensity was not significant.

Two-way analysis of variance was also used to examine the relationship between maturity status, infection intensity and the log (x+1) transformed weights of female *P. laevis* worms present. A significant difference existed in the weight of *P. laevis* recorded between stage I, II and III females (F ratio = 75.0; df = 2,732; $p \leq 0.0001$). A significant difference existed in the weights of female *P. laevis* recorded in low, medium and high intensity infections (F ratio = 14.6; df = 2,732; $p \leq 0.0001$), however the interaction between maturity status and infection intensity was not significant.

6.5.3 Comparison of the size of stage I, II and III female *P. laevis* between wild and stocked trout

Length

The mean length of stage I female *P. laevis* was 7.88mm($\pm$ 2.5) in wild trout and 8.35mm($\pm$ 2.2) in stocked trout, and the mean length of stage II worms was 8.31mm($\pm$ 2.1) in wild trout and 9.4mm($\pm$ 3.04) in stocked trout. For both stage I and II female *P. laevis* mean length values were higher for stocked trout (Tables 6.22-6.23; Fig 6.14).

Weight

The mean weight of stage I female *P. laevis* was 4.04mg($\pm$ 4.28) in wild trout and 2.8mg($\pm$ 2.7) in stocked trout. In wild and stocked trout mean weight values increased from stage I to stage II worms. The mean weight values for stage II worms were 4.29mg($\pm$ 2.1) in wild trout and 7.44mg($\pm$ 6.69) in stocked trout (Fig 6.15). Mean weight values for stage I female *P. laevis* were higher in wild trout, but for stage II female *P. laevis* mean weight values were higher in stocked trout (Tables 6.22-6.23).

Two-way analysis of variance was used to examine the relationship between maturity status (whether female *P. laevis* were stage I, II or III), fish host status (whether fish were wild or stocked) and the length of female *P. laevis* worms present. A significant difference existed in the length of *P. laevis* recorded between stage I, II and III females (F ratio = 135.5; df = 2,737; $p \leq 0.0001$). No significant difference existed in the lengths of female *P. laevis* recorded in wild or stocked trout, and the interaction between maturity status and fish host status was also not significant.

Two-way analysis of variance was also used to examine the relationship between maturity status, fish host status and the log (x+1) transformed weights of female *P. laevis* worms present. A significant difference existed in the weight of *P. laevis* recorded between stage I, II and III females (F ratio = 96.8; df = 2,736; $p \leq 0.0001$). No significant difference existed in the weights of female *P. laevis* recorded in wild or stocked trout, and the interaction between maturity status and fish host status was also not significant.

Finally, three-way analysis of variance was used to examine the relationship between month, fish host status (whether fish were wild or stocked), maturity status (whether female *P. laevis* were stage I, II or III) and the length of female *P. laevis* worms present. Significant differences in the lengths of female *P. laevis* existed between month (F ratio = 4.3; df = 3,724; $p \leq 0.005$) and maturity status (F ratio = 14.7; df = 3, 724; $p \leq 0.0001$). No significant difference existed in the lengths of female *P. laevis* between wild and stocked trout. There were significant interactions between month

and host status (F ratio = 25.8; df = 3,724; $p \leq 0.0001$) and month and maturity status (F ratio = 7.6; df = 6,724; $p \leq 0.0001$). However the interactions between host status and maturity status and the interactions between month, host status and maturity status were not significant.

Three-way analysis of variance was also used to examine the relationship between month, fish host status (whether fish were wild or stocked), maturity status (whether female *P. laevis* were stage I, II or III) and the log (x+1) transformed weight of female *P. laevis* worms present. A significant difference in the weight of female *P. laevis* existed between stage I, II and III females (F ratio = 17.2; df = 3, 723; $p \leq 0.0001$). No significant differences existed in the weight of *P. laevis* between months or between wild and stocked trout. There were significant interactions between months and host status (F ratio = 24.9; df = 3,723; $p \leq 0.0001$), and month and maturity status (F ratio = 7.8; df = 6,723; $p \leq 0.0001$). However the interactions between host status and maturity status and the interactions between month, host status and maturity status were not significant.

Table 6.19 Statistics summarising the length and weight distributions (in mm and mg respectively) of stage I female *P. laevis* in low, medium and high intensity infections in the total trout sample from Lough Feeagh.

	Low		Medium		High	
	Length	Weight	Length	Weight	Length	Weight
Count	102	102	78	78	301	301
Mean ($\pm$ S.D.)	8.72(2.93)	5.64(5.99)	7.79(2.11)	3.19(2.57)	7.97(2.17)	2.83(2.45)
Minimum	3	1	2	1	3	***
Maximum	20	40	13	15	15	24
Range	17	40	11	14	12	24

*** = The minimum weight was smaller than the lowest value recorded by the balance.

Table 6.20 Statistics summarising the length and weight distributions (in mm and mg respectively) of stage II female *P. laevis* in low, medium and high intensity infections in the total trout sample from Lough Feeagh.

	Low		Medium		High	
	Length	Weight	Length	Weight	Length	Weight
Count	24	24	12	12	77	77
Mean ($\pm$ S.D.)	8.21(2.24)	5.23(3.75)	8(1.54)	4.5(2.27)	8.46(2.2)	4.16(2.61)
Minimum	5	2	6	2	4	1
Maximum	13	16	10	9	15	16
Range	8	14	4	7	11	15

Table 6.21 Statistics summarising the length and weight distributions (in mm and mg respectively) of stage III female *P. laevis* in low, medium and high intensity infections in the total trout sample from Lough Feeagh.

	Low		Medium		High	
	Length	Weight	Length	Weight	Length	Weight
Count	45	45	12	12	91	91
Mean ($\pm$ S.D.)	12.77(13.1)	15.49(11.1)	10.66(1.45)	7.25(5.73)	11.81(2.56)	9.45(5.88)
Minimum	6	2	9	2	5	1
Maximum	20	40	14	21	18	31
Range	14	38	6	19	13	30

Table 6.22 Statistics summarising the length and weight distributions (in mm and mg respectively) of stage I, II and III female *P. laevis* in wild trout from Lough Feeagh.

	Stage I		Stage II		Stage III	
	Length	Weight	Length	Weight	Length	Weight
Count	264	264	108	108	148	148
Mean ($\pm$ S.D.)	7.88(2.5)	4.04(4.28)	8.31(2.1)	4.29(2.5)	12.01(2.7)	11.11(8.3)
Minimum	2	***	4	1	5	1
Maximum	20	41	15	16	20	40
Range	18	41	11	15	15	39

*** = The minimum weight was smaller than the lowest value recorded by the balance.

Table 6.23 Statistics summarising the length and weight distributions (in mm and mg respectively) of stage I, II and III female *P. laevis* in stocked trout from Lough Feeagh.

	Stage I		Stage II		Stage III†	
	Length	Weight	Length	Weight	Length	Weight
Count	217	217	5	5		
Mean ($\pm$ S.D.)	8.35(2.2)	2.8(2.7)	9.4(3.04)	7.44(6.69)		
Minimum	3	0.5	6	1		
Maximum	14	15	13	16		
Range	11	14.5	7	15		

† = No stage III female *P. laevis* in stocked trout.

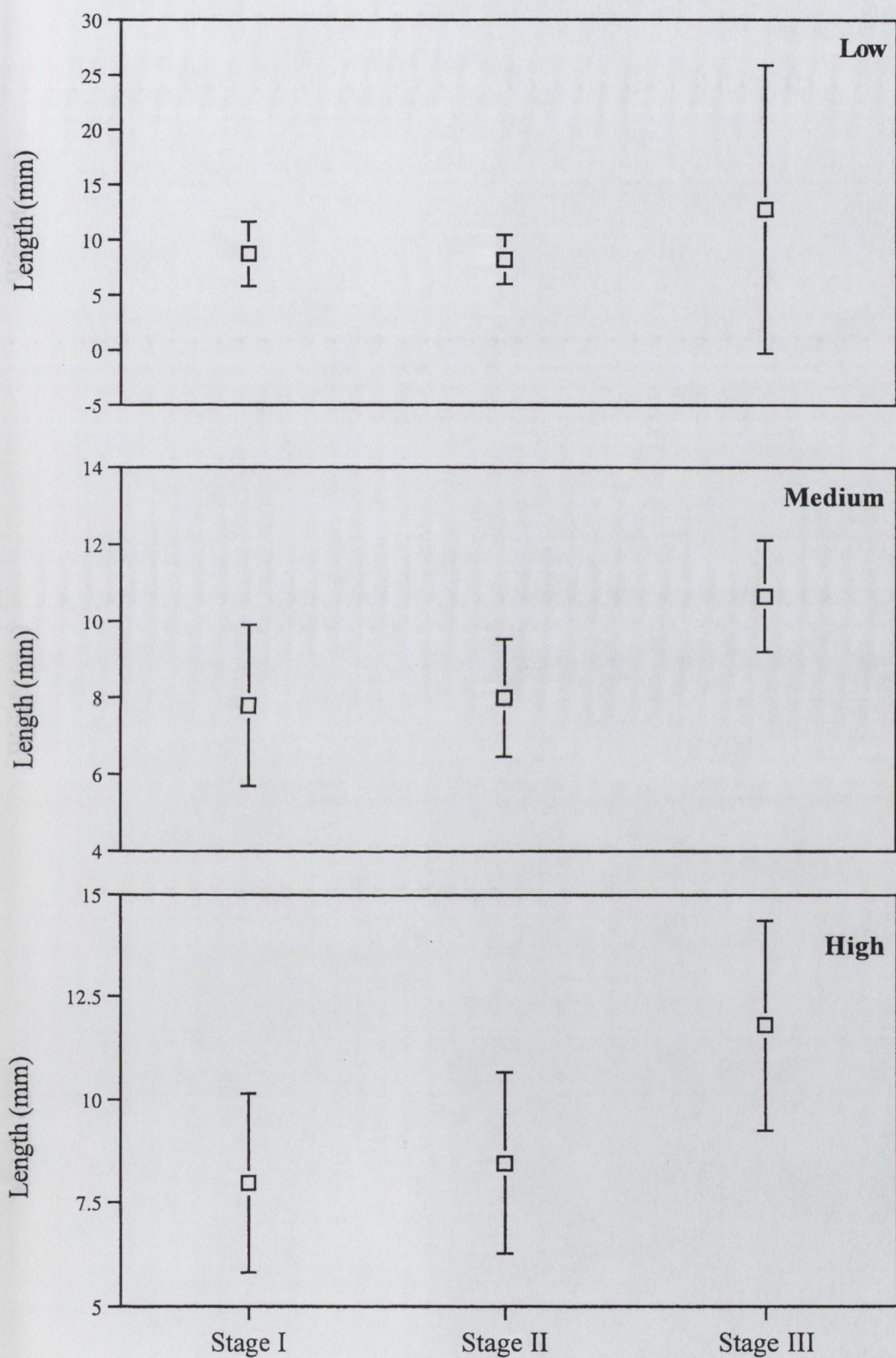


Fig 6.12 Mean length (+/- S.D.) of stage I, II and III female *P. laevis* in low, medium and high density infections in the total sample.

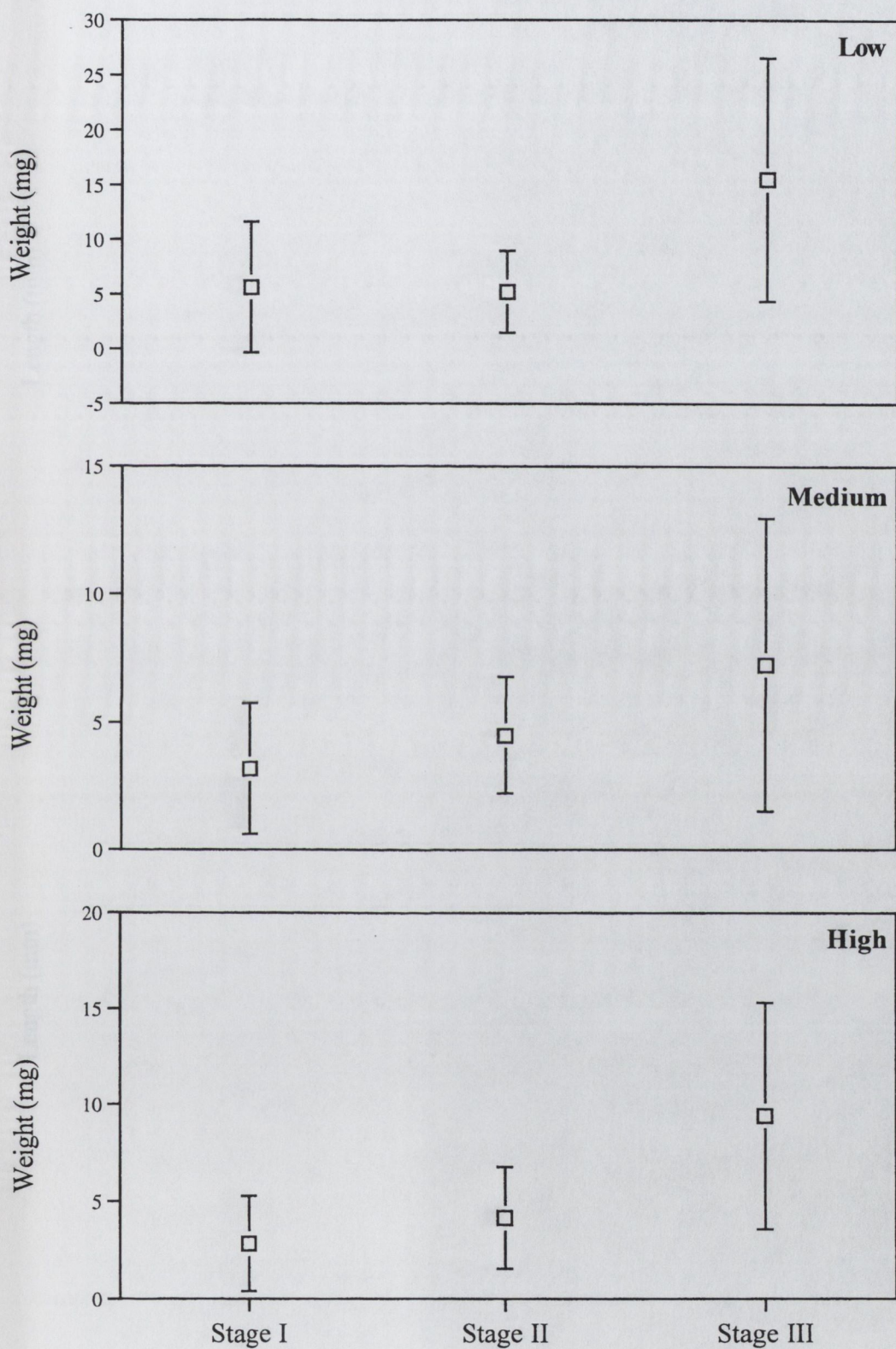


Fig 6.13 Mean weight (+/- S.D.) of stage I, II and III female *P. laevis* in low, medium and high intensity infections in the total sample.

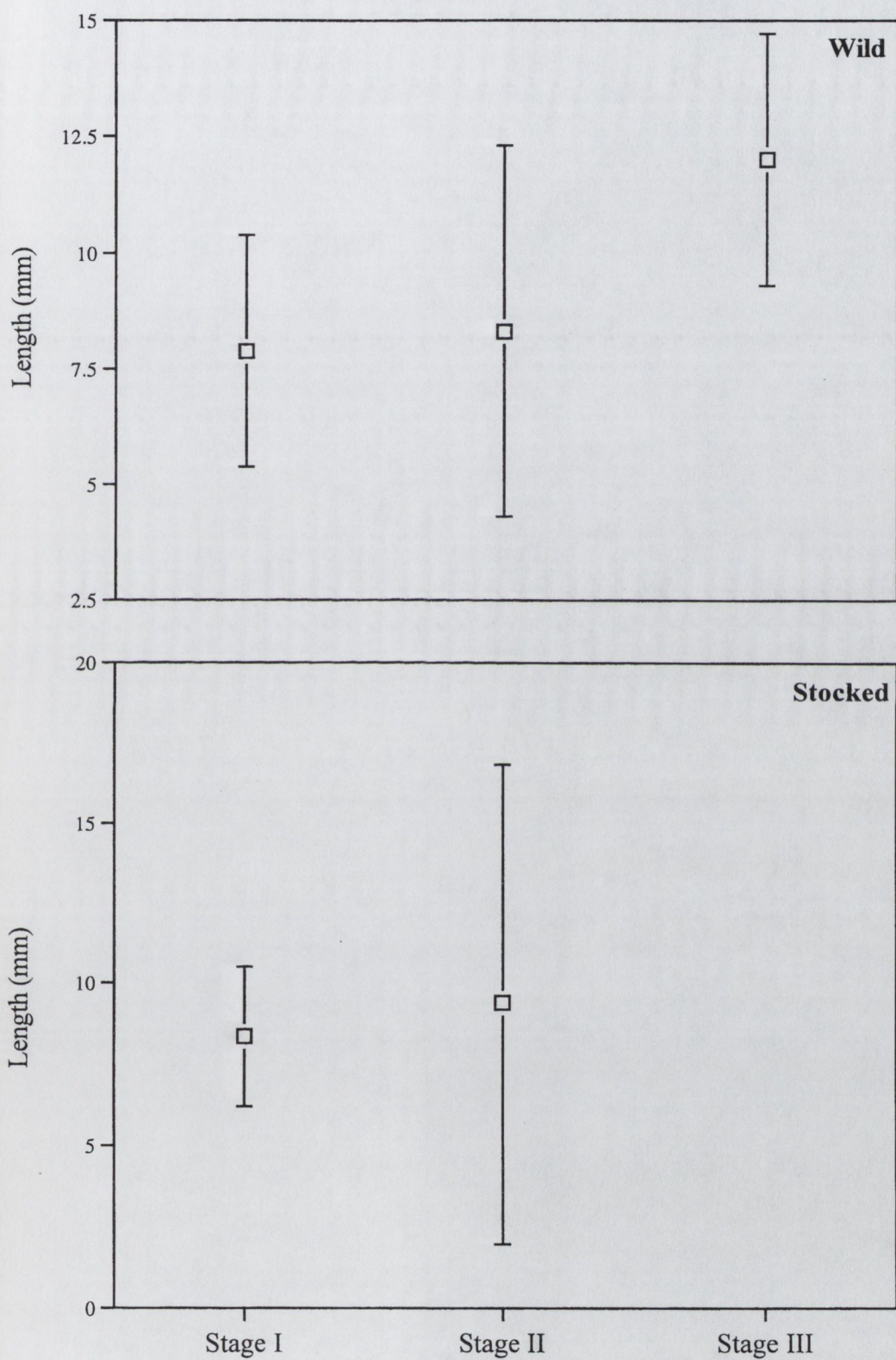


Fig 6.14 Mean lengths ($\pm$ S.D.) of stage I, II and III female *P. laevis* in wild and stocked trout. No stage III *P. laevis* were found in stocked trout.

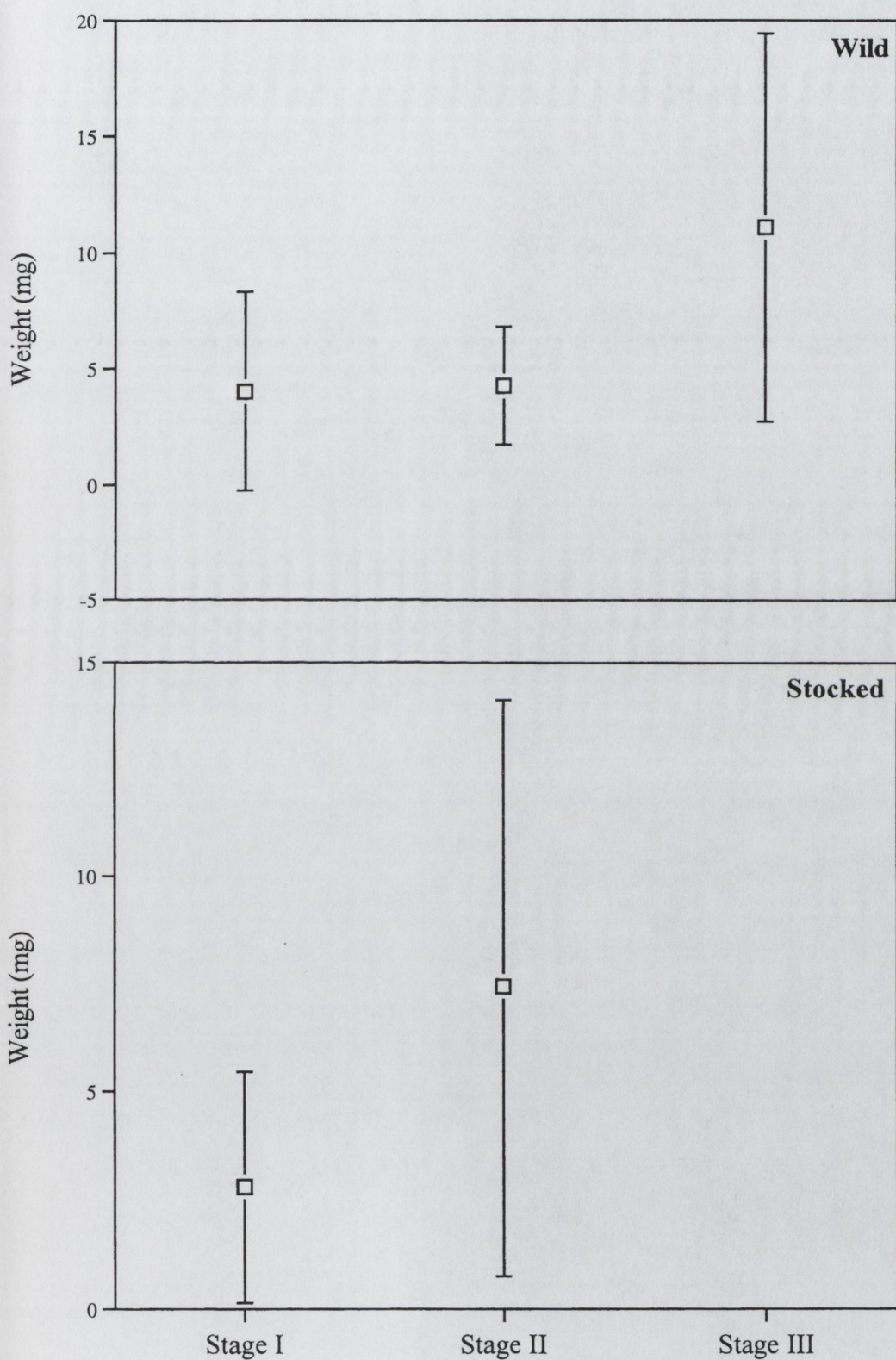


Fig 6.15 Mean weights ($\pm$ S.D.) of stage I, II and III female *P. laevis* in wild and stocked trout. No stage III *P. laevis* were found in stocked trout.

Table 4.30 Two sample t-Test and Mann-Whitney U-Test comparing the abundance of each parasite species found in the total sample of wild trout ($n = 257$) and stocked trout ($n = 122$).

2-sample t-Test of $\mu_1 - \mu_2$ on $\log(x+1)$ transformed data					Mann-Whitney U-Test Significance
Species	P - Value	t - Value	df	Sig.	
<i>Eubothrium crassum</i>	0.0001	-5.26	183	****	NS
<i>Crepidostomum farionis</i>	0.0001	5.59	349	****	NS
<i>Pomphorhynchus laevis</i>	0.0926	1.69	226	NS	***
<i>Acanthocephalus clavula</i>	0.0493	-1.98	216	*	NS
<i>Diphylobothrium ditremum</i>	0.0005	-3.55	156	***	***
<i>Rhabdochona sp.</i>	0.0649	-1.85	319	NS	NS
<i>Cystidicola farionis</i>	0.4183	-0.81	213	NS	NS
<i>Discocotyle sagittata</i>	0.7457	0.33	217	NS	NS
<i>Salmincola salmoneus</i>	0.5342	-0.62	294	NS	NS

df = degrees of Freedom; * = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$; **** = $P \leq 0.0001$; NS = not significant.

Table 4.31 Two sample t-Test and Mann-Whitney U-Test comparing the abundance of each parasite species found in the total sample of wild trout ($n = 64$) and stocked trout ($n = 47$) for the month of May.

2-sample t-Test of $\mu_1 - \mu_2$ on $\log(x+1)$ transformed data					Mann-Whitney U-Test Sig.
Species	P - Value	t - Value	df	Sig.	
<i>Eubothrium crassum</i>	0.0108	2.61	74	*	NS
<i>Crepidostomum farionis</i>	0.0001	6.05	78	****	NS
<i>Pomphorhynchus laevis</i>	0.0001	8.69	108	****	NS
<i>Acanthocephalus clavula</i>	0.5103	-0.66	104	NS	NS

df = degrees of Freedom; * = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$; **** = $P \leq 0.0001$; NS = not significant.

Table 4.32 Two sample t-Test and Mann-Whitney U-Test comparing the abundance of each parasite species found in the total sample of wild trout ($n = 88$) and stocked trout ($n = 25$) for the month of August.

2-sample t-Test of $\mu_1 - \mu_2$ on log (x+1) transformed data					Mann-Whitney U-Test Significance
Species	P – Value	t – Value	df	Sig.	
<i>Eubothrium crassum</i>	0.0001	-4.74	31	****	NS
<i>Crepidostomum farionis</i>	0.3771	0.89	46	NS	NS
<i>Pomphorhynchus laevis</i>	0.0001	7.26	90	****	NS
<i>Acanthocephalus clavula</i>	0.3198	-1.01	31	NS	NS
<i>Diphyllbothrium ditremum</i>	0.0613	-1.95	26	NS	***
<i>Rhabdochona sp.</i>	0.5069	-0.67	34	NS	NS
<i>Cystidicola farionis</i>	0.1615	-1.45	24	NS	NS
<i>Cystidicoloides tenuissima</i>	0.0310	-2.19	104	*	NS
<i>Discocotyle sagittata</i>	0.6741	0.42	35	NS	NS
<i>Salmincola salmoneus</i>	0.7897	0.27	51	NS	NS

df = degrees of Freedom; * = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$; **** = $P \leq 0.0001$; NS = not significant.

Table 4.33 Two sample t-Test and Mann-Whitney U-Test comparing the abundance of each parasite species found in the total sample of wild trout ($n = 45$) and stocked trout ($n = 50$) for the month of November.

2-sample t-Test of $\mu_1 - \mu_2$ on log (x+1) transformed data					Mann-Whitney U-Test Significance
Species	P – Value	t – Value	df	Sig.	
<i>Eubothrium crassum</i>	0.0001	-4.22	83	***	***
<i>Crepidostomum farionis</i>	0.5510	-0.59	92	NS	NS
<i>Pomphorhynchus laevis</i>	0.0001	-4.31	92	***	NS
<i>Acanthocephalus clavula</i>	0.6793	-0.41	89	NS	NS
<i>Diphyllbothrium ditremum</i>	0.0071	-2.76	88	***	NS
<i>Rhabdochona sp.</i>	0.3065	-1.03	90	NS	NS
<i>Cystidicola farionis</i>	0.0971	-1.68	67	NS	NS
<i>Discocotyle sagittata</i>	0.9965	-0.004	92	NS	NS
<i>Salmincola salmoneus</i>	0.2659	-1.12	84	NS	NS

df = degrees of Freedom; * = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$; **** = $P \leq 0.0001$; NS = not significant.

6.6 Examination of the niches of female *P. laevis* in each sample month and in the total sample

The distribution of the total sample of *P. laevis* (male and female worms) was previously examined in Chapter five, as was the distribution of the total sample of *P. laevis* in each sample month and in low, medium and high intensity infections.

In this section the distribution of female *P. laevis* along the intestine was examined for the total sample and for each sample month. In a similar manner to previous sections a set of statistics summarising the distribution of *P. laevis* along the intestine have been provided.

The distribution of female *P. laevis* was first examined for the total sample (Fig 6.16), this was then divided and the distribution of female *P. laevis* along the intestine was examined for each sample month (Figs 6.17-6.18) and at low, medium and high intensity infections (Fig 6.19).

6.6.1 Total sample of female *P. laevis* examined by month

The mean position of the total sample of female *P. laevis* was 76.76% (Table 6.23). Mean positions of female *P. laevis* decreased from a peak in April to the lowest value in November (Table 6.24). Median values also followed the same pattern.

Minimum values were comparable in April and May, they peaked in August and decreased to their lowest level in November. Maximum values were all 100%. Thus the level of the minimum value determined the range of female *P. laevis* along the intestine. The range of occurrence increased from April to May, decreased in August and peaked in November (Table 6.24).

25% quartile values increased from April to a peak in May and subsequently decreased to their lowest level in November. 75% quartile values decreased from a peak in April to their lowest value in November. Thus the interquartile range

decreased from a peak in April to the lowest value in August and then increased in November (Table 6.24).

Skewness values were negative and below one in April and November, positive in August and negative and above one in May. Kurtosis values were all positive. Thus the distribution of female *P. laevis* along the intestine was relatively peaked in all months, approximated a normal distribution in April, August and November but was negatively skewed in May (Table 6.24; Figs 6.17-6.18).

One-way analysis of variance showed significant differences in the location of female *P. laevis* along the intestine between sample months (F ratio = 63.5; df = 3,849; $p \leq 0.0001$). Least squares difference post hoc tests showed significant differences in location of female worms between November and every other month ($p \leq 0.0001$ in every case) and between August and April and August and May ($p \leq 0.0001$ in both cases).

6.6.2 Total sample of female *P. laevis* examined by intensity of infection

The total sample of female *P. laevis* was divided into low, medium and high intensity infections and the location of worms along the intestine was examined in each level.

The mean location decreased from a peak of 78.83% in low intensity infections to 77.83% in medium intensity infections and 75.71% in high intensity infections (Table 6.25; Fig 6.19). Median values were comparable between low and medium intensity infections, and lower for high intensity infections. Median values were lower than mean values in low intensity infections but higher than mean values in medium and high intensity infections (Table 6.25).

Minimum values decreased from low to medium intensity infections and increased in high intensity infections. In all cases the maximum value was 100%. Thus the range of occurrence of female *P. laevis* was primarily determined by the minimum values. The range of occurrence increased from low intensity infections to a peak in medium

intensity infections and subsequently decreased to its lowest level in high intensity infections (Table 6.25; Fig 6.19).

Both 25% and 75% quartile values decreased from low to high intensity infections. Thus low intensity infections had the highest 25% and 75% quartile values, and high intensity infections had the lowest 25% and 75% quartile values. However the interquartile range was almost identical for low and medium intensity infections but peaked for high intensity infections (Table 6.25; Fig 6.19).

Skewness values were negative and below one in low and high intensity infections, and negative and above one in medium intensity infections. Kurtosis values were all positive. Thus the distribution of female *P. laevis* along the intestine was peaked and approximated a normal distribution in low and high intensity infections, and peaked and negatively skewed in medium intensity infections (Fig 6.19).

One-way analysis of variance showed significant differences between the location of female worms along the intestine and the intensity of infection (F ratio = 6.2; df = 2,850; $p \leq 0.002$). Least squares difference post hoc tests showed significant differences in the location of female *P. laevis* along the intestine between high and low intensity infections ($p \leq 0.0008$).

Table 6.24 Summary statistics for the distribution of female *P. laevis* in the intestine of trout from Lough Feeagh for the total sample and for each month.

	April	May	August	November	Total
Count	145	231	172	305	853
Mean ($\pm$ S.D.)	82.07(9.58)	81.23(10.27)	77.29(7.83)	70.56(11.93)	76.76(11.45)
Median	81.4	79.85	76.1	70.65	76.61
Inter quartile	12.79	11.06	10.42	12.41	13.3
Range					
Minimum	47.2	44.6	56.1	31.49	31.49
Maximum	100	100	100	100	100
Range	52.8	55.4	43.9	68.51	68.51
Skewness	-0.43	-1.42	0.5	-0.32	-0.64
Kurtosis	1.19	8.91	0.56	0.93	2.08
Lower (25%)	75.51	76.36	72.67	64.57	70.7
Upper (75%)	88.3	87.42	83.09	76.98	84

Table 6.25 Summary statistics for the distribution of female *P. laevis* in the intestine of trout from Lough Feeagh at low (1-5 worms), medium (6-9 worms) and high (10+ worms) infection intensities.

	Low	Medium	High
Count	210	116	527
Mean ($\pm$ S.D.)	78.83(11.06)	77.83(11.28)	75.71(11.53)
Median	78.73	78.55	75.81
Inter quartile	12.22	12.29	14.38
Range			
Minimum	37.24	31.49	38.23
Maximum	100	100	100
Range	62.76	68.51	61.77
Skewness	-0.44	-1.02	-0.63
Kurtosis	1.25	2.44	2.33
Lower (25%)	72.9	72.62	68.93
Upper (75%)	85.12	84.91	83.3

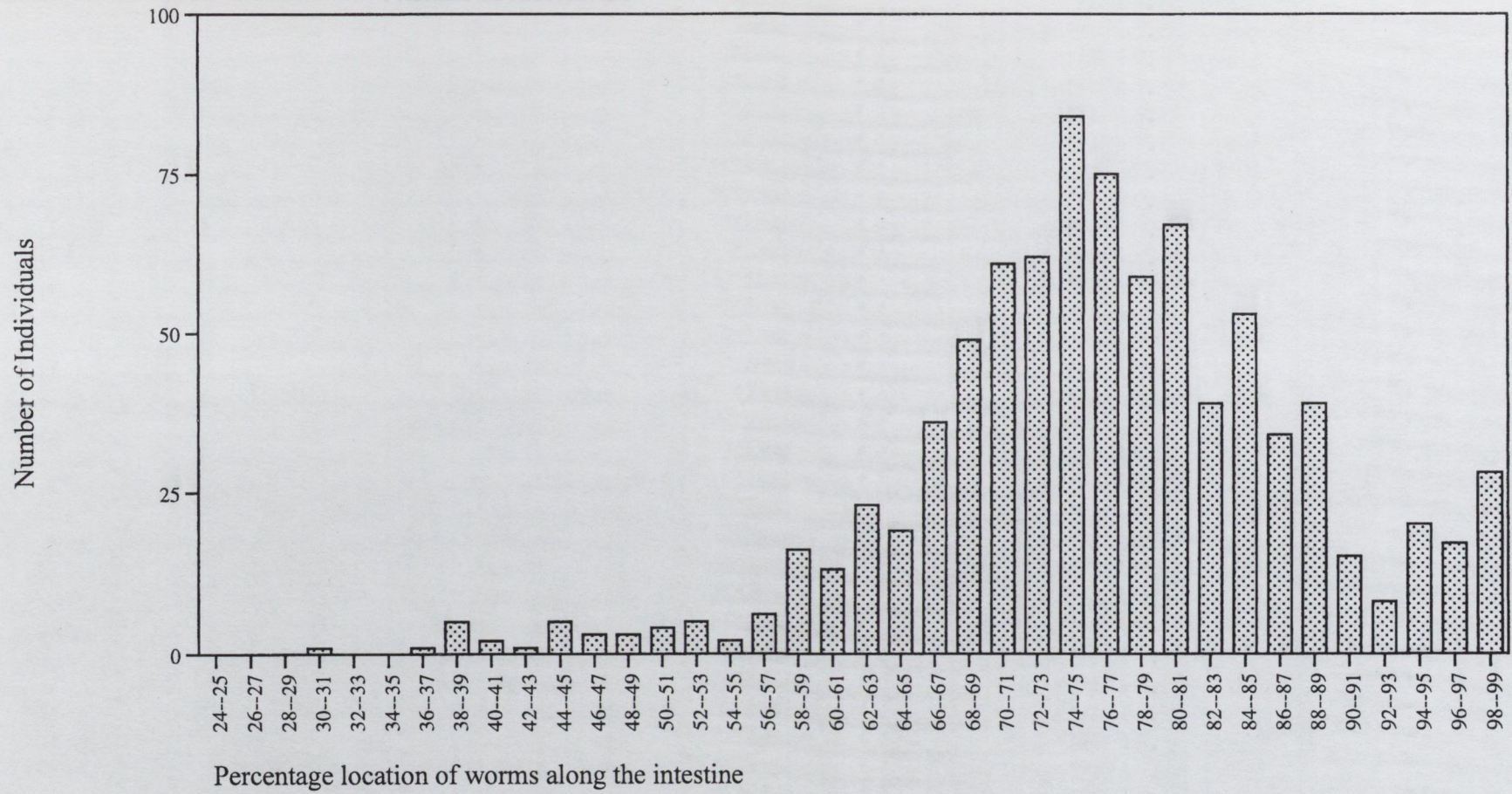


Fig 6.16 Fundamental niche of female *P. laevis* along the intestine of trout from Lough Feeagh.

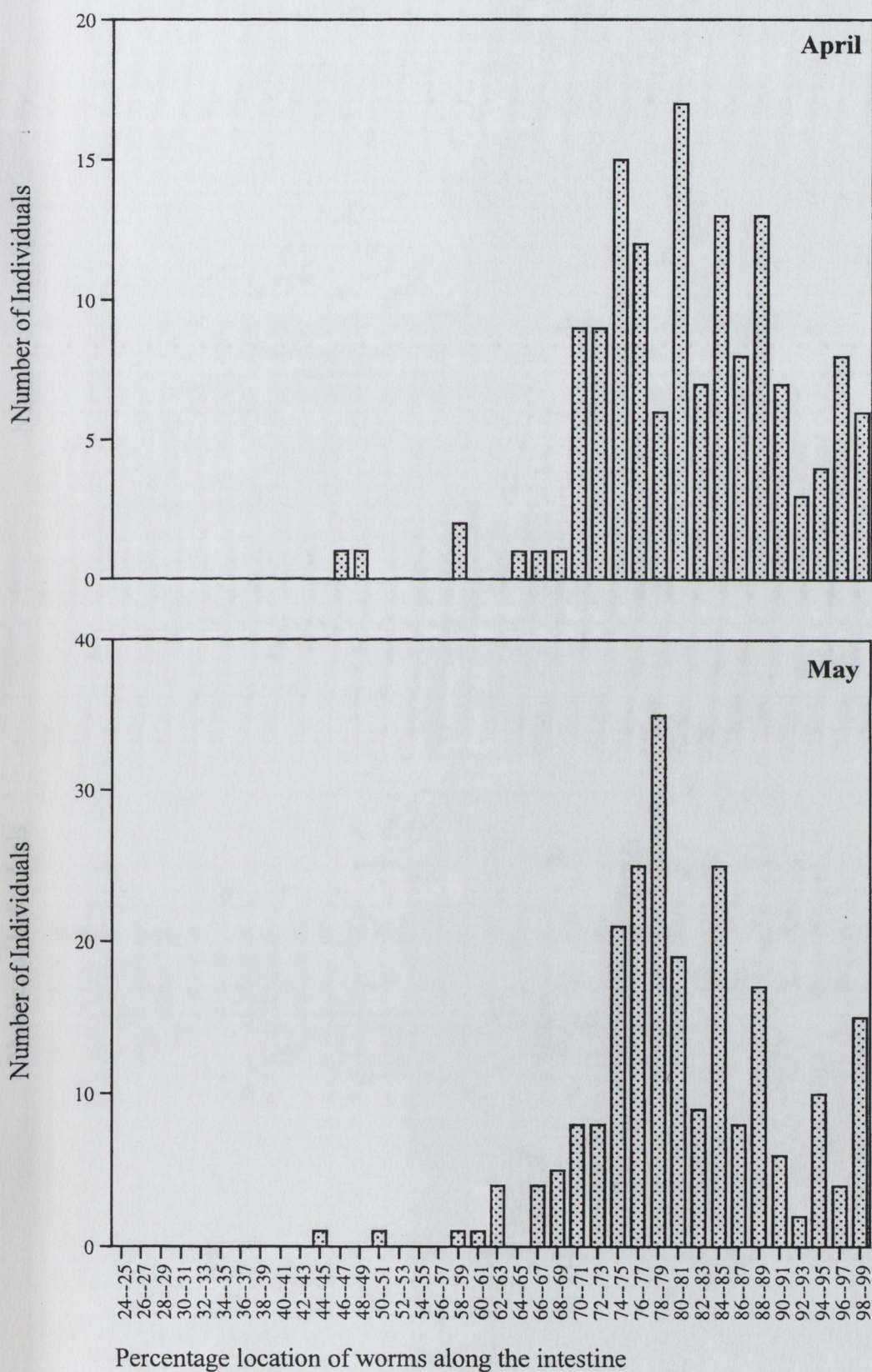


Fig 6.17 Niches of female *P. laevis* along the intestine of trout in Lough Feeagh in April and May.

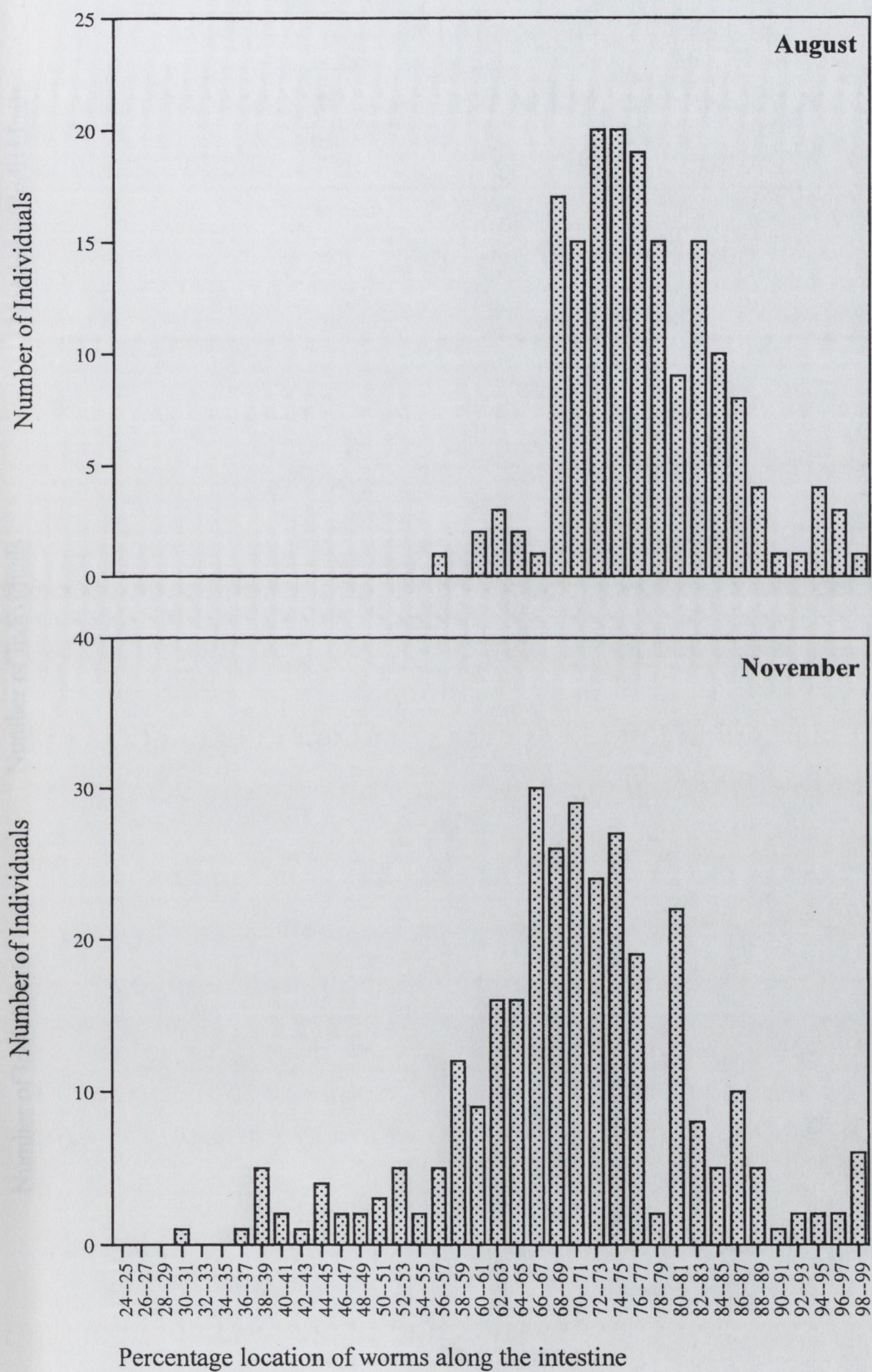


Fig 6.18 Niches of female *P. laevis* along the intestine of trout in Lough Feeagh in August and November.

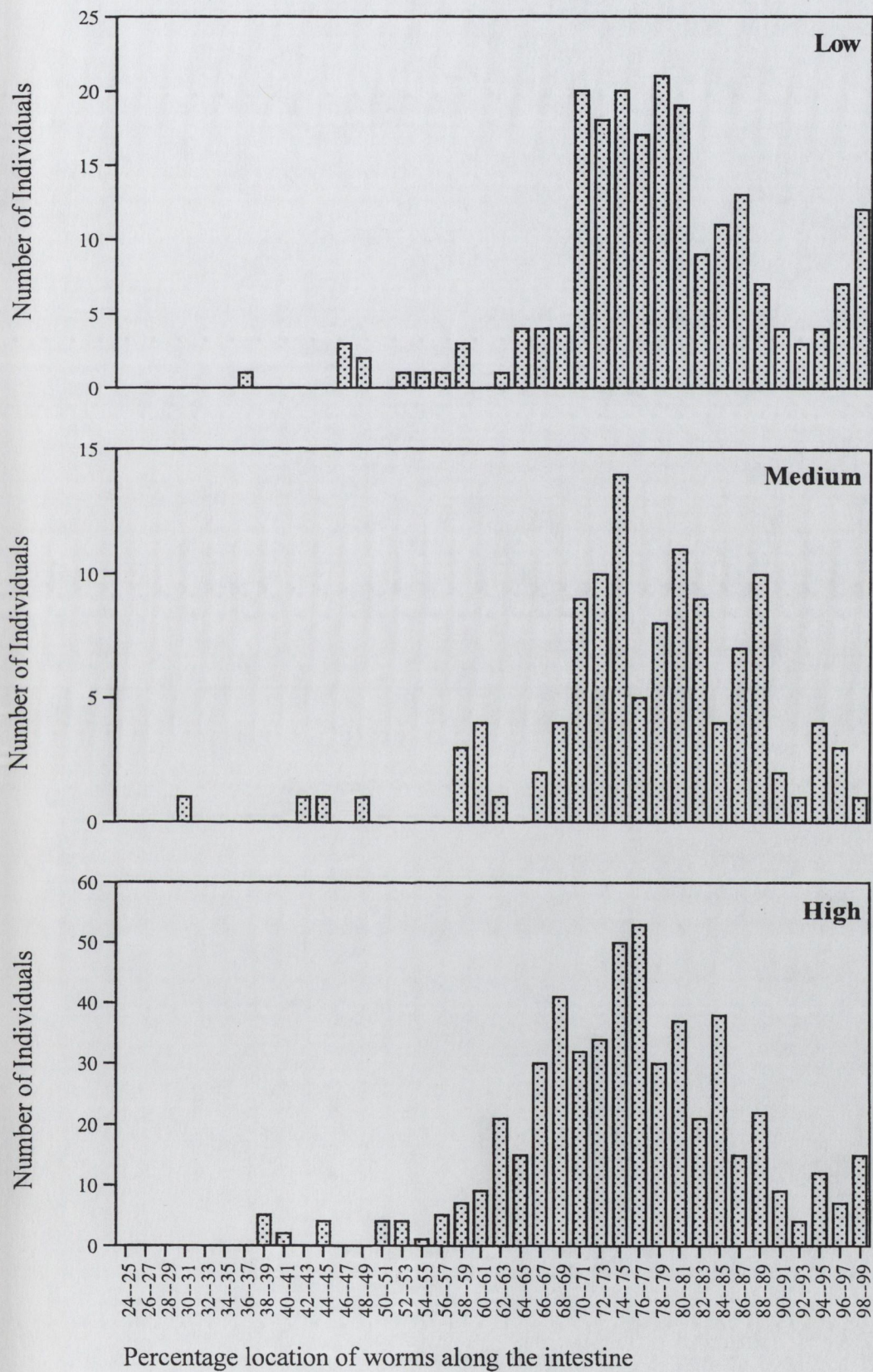


Fig 6.19 Niches of female *P. laevis* in low intensity (1-5 worms), medium intensity (6-9 worms) and high intensity (10+ worms) infections along the intestine of trout from Lough Feeagh.

6.7 Examination of the niches of stage I, II and III female *P. laevis* in the total sample of trout from Lough Feeagh

In this section the distributions of stage I, II and III female *P. laevis* along the intestine were examined for the total trout sample in Lough Feeagh. In a similar manner to previous sections a set of statistics summarising the distribution of *P. laevis* along the intestine have been provided.

The mean location values increased from 75.09% for stage I female *P. laevis* to a peak of 81.48% for stage II female *P. laevis* and subsequently decreased to 77.93% for stage III female *P. laevis* (Table 6.26; Fig 6.20). Median values followed a similar pattern.

Minimum location values increased from stage I *P. laevis* to a peak for stage II *P. laevis* and for stage III females. Maximum values were 100% for stage I females and 98.8% and 98.9% for stage II and III female *P. laevis* respectively. Thus the range of occurrence decreased from stage I to stage II female *P. laevis* and then increased for stage III female *P. laevis* (Table 6.26; Fig 6.20).

25% and 75% quartile values increased from stage I female *P. laevis* to a peak for stage II *P. laevis* and subsequently declined again for stage III female *P. laevis*. However the interquartile range decreased from stage I to stage III female *P. laevis* (Table 6.26; Fig 6.20).

Skewness values were negative and below one for stage I female *P. laevis*, zero for stage II female *P. laevis* and positive and below one for stage III female *P. laevis*. Kurtosis values were positive for stage I and III female *P. laevis* and negative for stage II female *P. laevis*. Thus the distributions of female *P. laevis* along the intestine were peaked but approximated normal for worms of stage I and III maturity and flattened but approximated normal for worms of stage II maturity (Table 6.26; Fig 6.20).

One-way analysis of variance showed significant differences in the positions of stages I, II and III female *P. laevis* along the intestine (F ratio = 17.3; df = 2,735; $p \leq 0.0001$). Least squares difference post hoc tests showed significant differences between the positions of stage I and II female *P. laevis* ($p \leq 0.0001$), stage III and stage I female *P. laevis* ($p \leq 0.005$) and stage III and stage II female *P. laevis* ($p \leq 0.008$).

Table 6.26 Summary statistics for the distribution of stage I, II and III female *P. laevis* in the intestine of the total sample from Lough Feeagh for the total sample and for each month.

	Stage I	Stage II	Stage III
Count	479	113	148
Mean ($\pm$ S.D.)	75.09(12.16)	81.48(7.74)	77.93(7.11)
Median	75.4	80.92	76.63
Inter quartile	14.14	9.89	9.09
Range			
Minimum	31.49	59	56.1
Maximum	100	98.8	98.9
Range	68.51	39.8	42.8
Skewness	-0.33	0	0.45
Kurtosis	0.62	-0.03	0.71
Lower (25%)	68.54	75.89	73.65
Upper (75%)	82.68	85.79	82.74

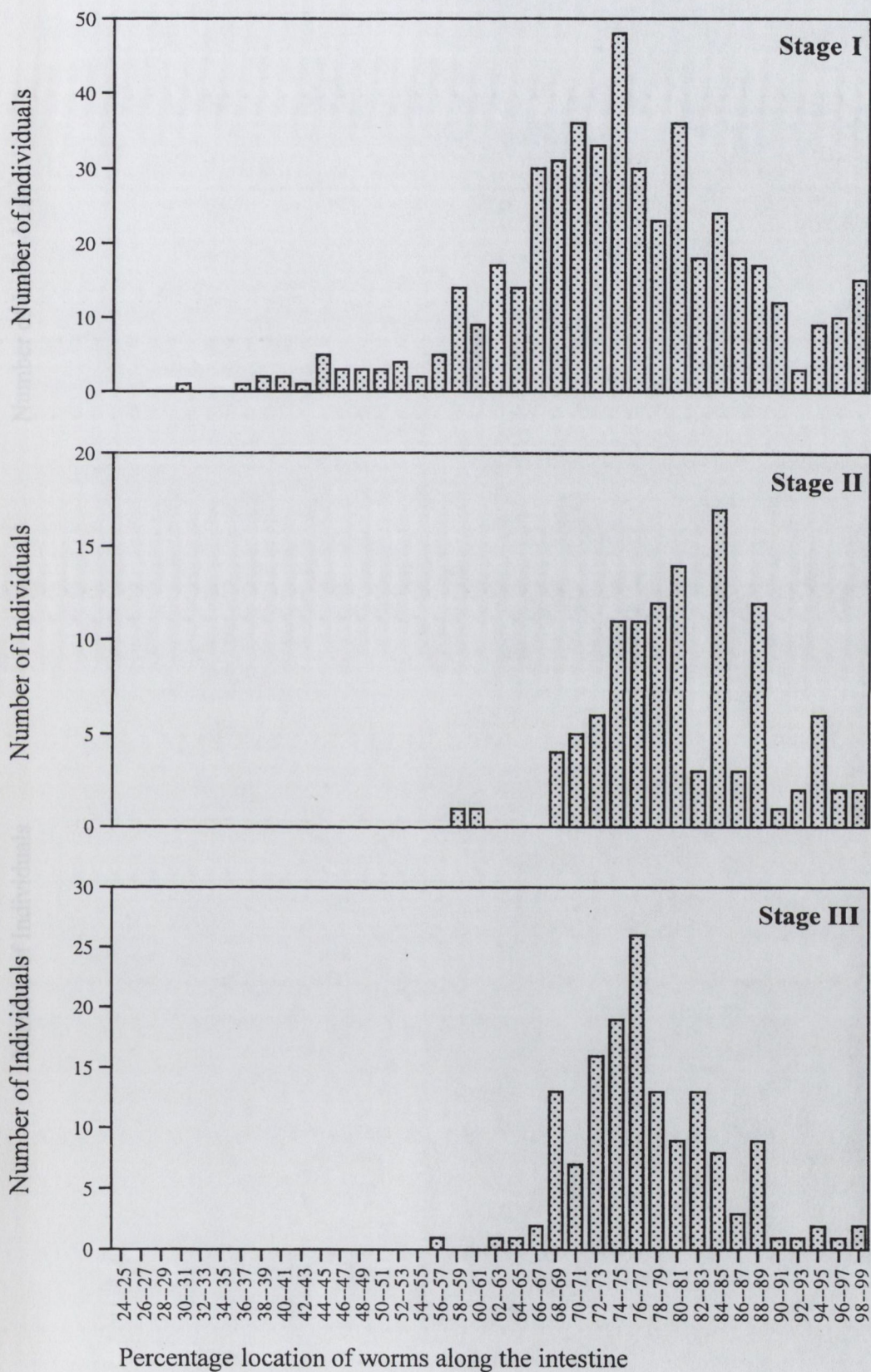


Fig 6.20 Fundamental niches of stage I, II and III female *P. laevis* along the intestine of trout from Lough Feeagh.

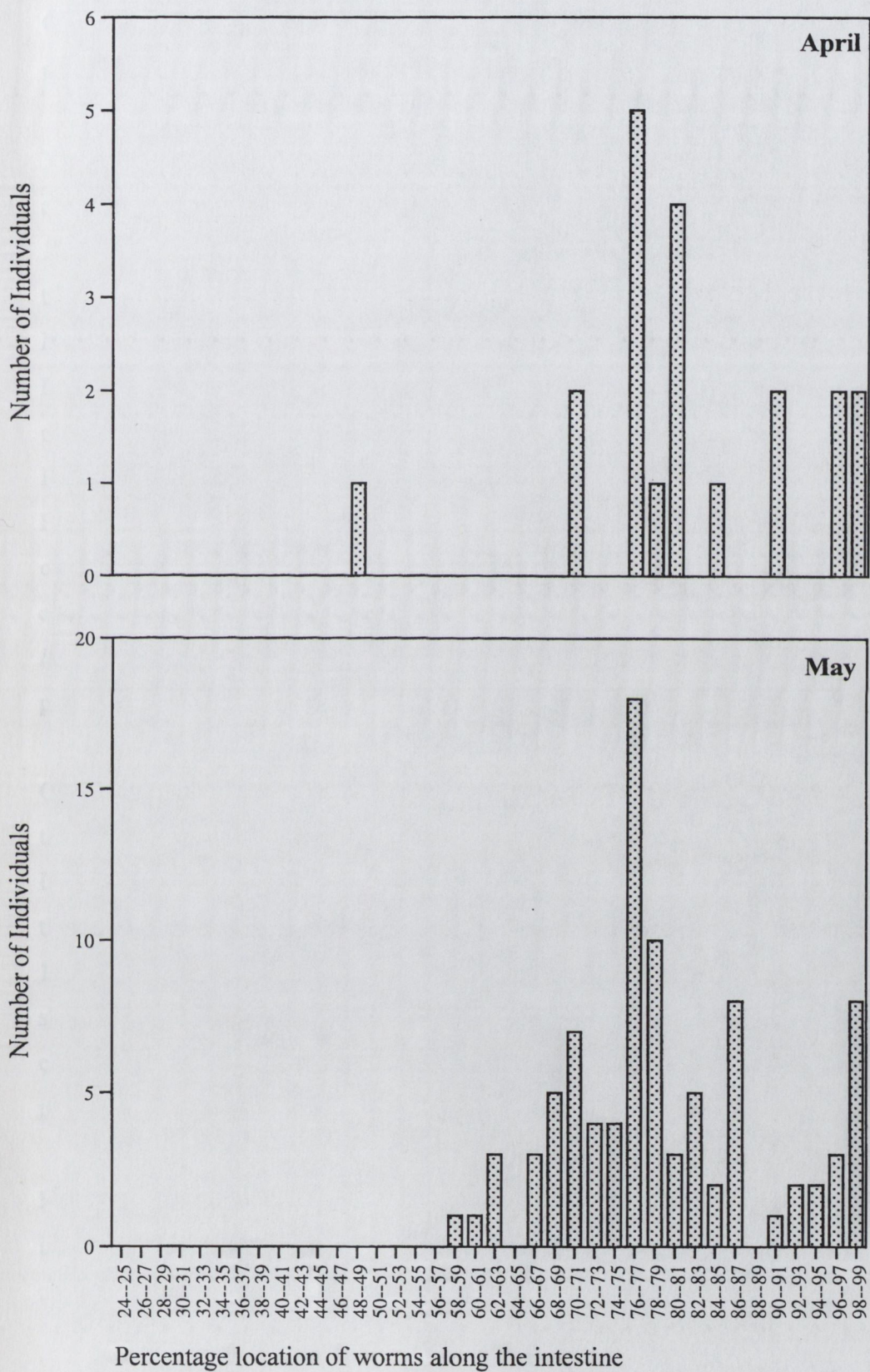


Fig 6.21 Niches for stage I female *P. laevis* along the intestine of trout in Lough Feeagh in April and May.

6.8 Discussion

Q. Are the *P. laevis* parasites from this sample characteristic of the Irish strain of *P. laevis* in terms of size and reproductive status?

The acanthocephalan *P. laevis* is widely distributed and abundant in both salmonid and non-salmonid fish in Ireland (Holland and Kennedy, 1997; Kane, 1966; Kennedy, 1974b). Particularly prevalent and intense infections have been recorded from brown trout from a variety of river systems (Conneely and McCarthy, 1984; Fitzgerald and Mulcahy, 1983; Molloy *et al.*, 1995a). The pattern of distribution of *P. laevis* in Ireland is strikingly different from that of mainland Britain where it has only been described, with any frequency, from three river systems (Kennedy *et al.*, 1978). Furthermore, *P. laevis* also utilises different intermediate and definitive hosts in Britain and Ireland. In Britain it uses *Gammarus pulex* as an intermediate host and cyprinids, such as chub and barbel as definitive hosts. In this situation, brown trout act as a secondary host. In contrast, in Ireland where chub and barbel are absent, *P. laevis* utilises *Gammarus duebeni* as an intermediate host and brown trout act as preferred definitive hosts.

On the basis of these distributional and ecological differences it has been proposed that *P. laevis* exists as three discrete, biologically specialised strains - a widespread Irish strain, a highly localised English freshwater strain and a marine strain found in the Baltic and coastal regions of the North Sea and English channel (Kennedy *et al.*, 1978, 1989; Kennedy, 1984a). Kennedy *et al.* (1989) also hypothesised that the Irish strain was likely to be more recent, having been introduced into Ireland with cyprinids. The changes in intermediate and definitive hosts may have exerted the necessary selection pressure to evolve a separate strain.

Recently Kennedy (1996c) provided evidence that *P. laevis* colonised and established in a small Devon river where chub and barbel were absent and instead used brown trout as a preferred definitive host. This observation gives support to the hypothesis

that *P. laevis* was introduced from Britain to Ireland and subsequently adapted to brown trout in the Irish situation. Despite the ecologically interesting differences observed between the Irish and English strain of *P. laevis*, quantitative data on the population biology of the parasite, and in particular on maturity status, is still scarce.

Molloy *et al.* (1995b) examined the population biology of 731 *P. laevis* from the west of Ireland, 510 females and 221 males. Parasites ranged in length from 1 to 20mm with a mean of 7mm, and most parasites weighed between 1 and 10mg with a mean of 7mg. The authors also reported that the length and weight of parasites varied with the season, and that longer and heavier parasites were found in summer. In this study the mean length value recorded for the total sample of *P. laevis* was 8.5mm and parasites also ranged in length from 1 to 20mm. The mean weight value for the total sample was 4.6mg and the range in weight was from less than 1mg to 51mg.

Thus, the length values recorded for *P. laevis* were comparable between this study and that of Molloy *et al.* (1995b) whereas the mean weight value was lower for this study. Results from this study also suggest that there was some seasonal variation in the length and weight of *P. laevis*, as the mean length and weight values were highest in August. The seasonal variation in the lengths and weights of *P. laevis* could explain the discrepancy in the mean weight values between this study and that of Molloy *et al.* (1995b). In this study a large number of *P. laevis* were examined outside the peak summer season. Mean weight values increased from 3.7mg in May to 9.2mg in August and then decreased to 3mg in November.

The size range of *P. laevis* from Irish brown trout in the present study is lower than that of Molloy *et al.* (1995b), possibly for the reasons described above, but it corresponds well with that recorded by Brown (1989) from parasites in chub collected from the rivers Severn and Worfe (Table 6.27). Parasite weights were also similar to those attained by *P. laevis* recovered from chub and barbel in the River Avon (Table 6.27) but contrasted with the lower weights recorded from brown trout in the same location (Kennedy *et al.*, 1989).

For the total sample of female *P. laevis* 65% of worms were of stage I maturity, 15% were of stage II maturity and 20% were of stage III maturity. The same pattern was found for each of the monthly samples, with the exception of August when the majority of worms, 76%, were of stage III maturity. Molloy *et al.* (1995b) reported a similar proportion (17%) of gravid female *P. laevis* in brown trout in Ireland. Kennedy *et al.* (1978) reported that 14.7% of the total sample of *P. laevis* in brown trout and 17.6% of the total sample of *P. laevis* in rainbow trout were gravid.

Table 6. 27 Size attained by *P. laevis* in a variety of hosts from Britain and Ireland.

Fish Host	Location	Parasite maximum size (mg)	Parasite size range (mg)	Source
<i>L. cephalus</i>	R. Severn & Worfe	> 90	<10->90	Brown (1989)
<i>L. cephalus</i> & <i>B. barbus</i>	R. Avon	N/A	7-10	Kennedy <i>et al.</i> (1978)
<i>S. gairdneri</i>	R. Avon	7.4	N/A	Kennedy <i>et al.</i> (1978)
<i>S. trutta</i>	R. Avon	3	N/A	Kennedy <i>et al.</i> (1989)
<i>S. trutta</i>	L. Feeagh & Bunaveela Lake	100	1-100	Molloy <i>et al.</i> (1995b)
<i>S. trutta</i>	L. Feeagh	51	<1-51	Byrne (This study)

N/A = Not available

However, Hine and Kennedy (1974) reported that 58-80% of the female worms recovered from chub in the River Avon were gravid. Therefore the value recorded for the proportion of mature parasites in brown trout in this study (20%) was relatively low. Some factors were found to influence maturity status including season of host capture, and length of parasite. Immature parasites were more abundant in winter and early spring with an increase in mature parasites in summer. In contrast, Hine and Kennedy (1974) found no evidence of a pronounced seasonal cycle in the maturity status of *P. laevis* in chub. In addition, larger parasites tended to harbour a greater proportion of mature and maturing acanthors. Munro *et al.* (1989) also found a relationship between increasing *P. laevis* trunk length and the proportion of stage III females in flounder.

Table 6.28 provides comparative data on the proportion of stage III parasites from brown trout, rainbow trout and chub in England and Ireland. It can be seen that the proportion of stage III female parasites in the Irish brown trout sample is low compared to that recorded from chub in Britain (Brown, 1989), a little higher than that observed in brown trout sampled from Britain (Kennedy *et al.*, 1978) and comparable to rainbow trout from the same location (Kennedy *et al.*, 1978). Kennedy (1996c) also provided data on the proportion of gravid females of *P. laevis* in brown trout from a small English river which showed evidence of colonisation and spread of the acanthocephalan over an 11 year period. Strikingly, in the absence of chub and barbel, 71% of the female parasites were gravid illustrating that in this situation brown trout are the preferred definitive host for the English strain (see Table 6.28).

Hine and Kennedy (1974) divided hosts of *P. laevis* into three groups; natural or preferred hosts in which *P. laevis* attains maximum growth and gravid parasites are common; hosts in which some growth is possible and a few parasites become gravid; and a third group where no growth or maturity is possible. On the basis of this classification, chub, barbel and rainbow trout were found to be preferred definitive hosts for the English strain of *P. laevis* over brown trout, dace and grayling (Hine and Kennedy, 1974; Kennedy *et al.*, 1978). This sample of Irish brown trout appears to fit the description of natural or preferred host of *P. laevis* in terms of parasite size. Despite these size considerations, only a moderate proportion of worms of the Irish strain attained stage III maturity status compared to parasites from chub in Britain (Brown, 1989). Furthermore, the production of mature acanthors fluctuated substantially throughout the year. Therefore on the basis of maturity status, this sample of Irish brown trout appears to fall within the second host category.

Using this data set it was also possible to examine whether the niches of female *P. laevis* of stage I, II and III maturity differed from that of the total sample of female *P. laevis*. In all cases the mean position values for female *P. laevis* of stage I, II and III maturity were comparable to the mean position values for the total female sample of *P. laevis*. The range of occurrence values for female *P. laevis* of stage I, II and III

Table 6.28 Maturity status of *P. laevis* in a variety of fish hosts from Britain and Ireland.

Fish Host	Location	No. of fish examined	% Infected	Range	Proportion of stage III females (%)	Seasonal range of stage III females (%)	Source
<i>L. cephalus</i>	R. Severn & Worfe	216	100	1-207	N/A	60-72	Brown (1989)
<i>S. gairdneri</i>	R. Avon	15	93.3	1-52	17.6	N/A	Kennedy <i>et al.</i> (1978)
<i>S. trutta</i>	R. Avon	19	78.5	1-141	14.7	N/A	Kennedy <i>et al.</i> (1978)
<i>S. trutta</i>	R. Otter	12	100	2-54	71	N/A	Kennedy (1996)
<i>S. trutta</i>	L. Feeagh & Bunaveela Lake	549	58	0-42	17	3.5-33.3	Molloy <i>et al.</i> (1995)
<i>S. trutta</i> †	L. Feeagh	379	62.3	0-80	20	4.3-76	Byrne (This Study)

N/A = Not available; † = Refers to wild and stocked trout.

maturity were also comparable to the range of occurrence values recorded for the monthly female *P. laevis* samples.

Therefore it can be concluded that there was no difference between distributions of stage I, II and III female *P. laevis* and the total sample of female *P. laevis*, or between stage I, II and III female *P. laevis* and the overall total sample of *P. laevis* (both male and female worms combined). The random nature of the establishment and attachment of *P. laevis* along the intestine of trout, as described by Kennedy *et al.* (1976), and the fact that *P. laevis* does not move once attached, accounts for the lack of any major differences between the intestinal distributions of stage I, II and III female *P. laevis* and the total sample of female *P. laevis* and the total overall *P. laevis* sample (male and female worms combined).

Q. Is the size and reproductive status of *P. laevis* comparable between wild and stocked trout?

No other published studies have compared the reproductive biology of *P. laevis* between wild and stocked trout. When the lengths and weights of *P. laevis* were compared between wild and stocked trout, total mean length (8.5mm) and mean weight (5.3mg) values were higher for wild trout (Table 6.11; Table 6.12). However, mean length and weight values were higher for stocked trout in April (10.1mm, 7.1mg respectively) and mean weight values were higher for stocked trout in May (3.8mg). For all other parameters values were higher in wild trout. The lengths and weights of *P. laevis* in low, medium and high intensity infections were also compared between wild and stocked trout and in this case all values were higher for wild trout. There were a number of fluctuations in the size of *P. laevis* between wild and stocked trout for each sample month, but these changes were not mirrored in terms of maturity status (Tables 6.11-6.12; Tables 6.14-6.15).

It is possible that the differences in the lengths and weights recorded for *P. laevis* in wild and stocked trout between months were related to the number of parasite

individuals present (Table 6.11; Table 6.12). Brown (1986) reported that density dependent parasite establishment and survival occurred such that the number of parasites which survived to reproduce within an individual fish reached a ceiling level. Also, a number of other workers have reported that acanthocephalans extend their distributional range at higher intensities of infection (Awachie, 1966; Amin, 1975; Muzzall, 1980). Therefore, it would be reasonable to assume that as the number of parasite individuals recorded in an individual fish increased, the mean length and weight values decreased. This could explain the pattern of occurrence of *P. laevis* in wild and stocked trout between months.

However, when the lengths and weights of *P. laevis* were compared between low, medium and high intensity infections a different pattern emerged. If the theory proposed for the monthly samples was correct, one would expect that in all cases stocked trout would have greater length and weight values for *P. laevis*, because fewer *P. laevis* were found in stocked trout. This was not the case, the opposite situation occurred, in all cases wild trout had greater length and weight values for *P. laevis*.

Kennedy (1974a) reported considerable variation in the numbers of *P. laevis* establishing in goldfish at the same time after infection, despite the fact that there was very little variation in the number of cystacanths given to each fish. He concluded that the variation must have been due to differences between individual fish with respect to conditions in the alimentary canal affecting cystacanth eversion or general susceptibility to infection.

Thus it appears that there are a number of possible explanations for the striking differences in the maturity status of female *P. laevis* between wild and stocked trout. It is possible that the size of *P. laevis* recorded in stocked trout was responsible for the lack of gravid females. Molloy *et al.* (1995b) reported that longer and heavier worms, thus more gravid females, were recorded in summer. In this sample, the mean lengths and weights of female *P. laevis* were lower in stocked trout in summer. It is

also possible that the scarcity of male *P. laevis* in stocked trout, meant that fewer female *P. laevis* matured. In wild trout 519 male *P. laevis* were recorded in the total sample, 69 in April, 204 in May, 145 in August and 101 in November, in contrast 143 male *P. laevis* were found in the total sample in stocked trout. 18 in May, 1 in August and 124 in November.

Also, in the chapter five it was suggested that variation of conditions in the intestine of stocked trout were more favourable for *P. laevis*, resulting in worms being liberated sooner and hence having a more anterior position. It is possible that some other factors, possibly physiological factors, were affecting the growth of *P. laevis* in stocked trout, resulting in the smaller length and weight values for stocked trout.

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Chapter 7

Examination of the co-occurrence of *P. laevis* and *A. clavula* in brown trout in Lough Feeagh

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7.1 Organisation of chapter seven

In chapter seven the population biology of *P. laevis* in single infections and concurrent infections with *A. clavula* is discussed. The chapter is divided into five sections.

In the first section the population biology characteristics of *P. laevis* in single and concurrent infections with *A. clavula* were examined. The mean number of *P. laevis* occurring alone and in concurrent infections with *A. clavula* was examined. Kendall's tau non-parametric correlation co-efficient was used to examine the relationship in abundance between *P. laevis* and *A. clavula*, and chi-squared analysis was used to examine the relationship between the intensity of *P. laevis* and *A. clavula*.

In the second section the sizes of *P. laevis* in single and concurrent infections with *A. clavula* were compared for the total sample and for each sample month. The sizes of *P. laevis* in single and concurrent infections with *A. clavula* were then compared in low, medium and high intensity infections.

In section three the size of female *P. laevis* in single and concurrent infections with *A. clavula* were compared for the total sample and for each sample month. And the sizes of female *P. laevis* in single and concurrent infections with *A. clavula* were compared in low, medium and high intensity infections.

In section four the lengths and weights of female *P. laevis* in stage I, II and III maturity were compared between *P. laevis* in single and concurrent infections, and in the final section of this chapter the niches of *P. laevis* occurring alone and co-occurring with *A. clavula* were compared for the total sample and for each sample month

7.2 The population biology characteristics of *P. laevis* in single infections and concurrent infections with *A. clavula*

A total of 1319 *P. laevis* occurred in the absence of *A. clavula* in Lough Feeagh (Table 7.1). The mean number of *P. laevis* worms occurring alone in infected fish increased substantially from April to May, decreased in August and subsequently increased in November (Table 7.1). A total of 401 *P. laevis* co-occurred with *A. clavula* in Lough Feeagh. The mean number of *P. laevis* worms co-occurring with *A. clavula* in infected fish increased from April to a peak in May, decreased to the lowest level in August and subsequently increased again in November (Table 7.1).

Two-way analysis of variance was used to examine the relationship between month, infection status of *P. laevis* (whether worms were present as single or concurrent infections) and the total number of *P. laevis* present in Lough Feeagh. A significant difference existed in the numbers of *P. laevis* recorded in each month (F ratio = 83.6; df = 3,1712; $p \leq 0.0001$). A significant difference also existed in the number of *P. laevis* recorded between single and concurrent infections (F ratio = 13.7; df = 1,1712; $p \leq 0.0002$) in each month and for the total sample the mean number of *P. laevis* was higher when it occurred alone. Finally the interaction between the month and the infection status of *P. laevis* was also significant (F ratio = 16.3; df = 3,1712; $p \leq 0.0001$). Month was the most significant factor in this two-way analysis.

Kendall's tau, a non-parametric correlation co-efficient was used to assess the relationship in abundance between the total sample of *P. laevis* and *A. clavula*. A significant negative correlation existed between the abundance of *P. laevis* and *A. clavula* ($\tau = -0.97$; $p = 0.021$). On the basis of this evidence it could be concluded that the presence of *P. laevis* in a fish had a negative effect on the presence of *A. clavula* in the same fish.

The relationship between the intensity of *P. laevis* and *A. clavula* was also examined. Chi-squared analysis could not be used to look at the relationship between uninfected,

and low and high intensity infections because the main underlying assumption of the test statistic, that the value of any individual cell should not fall below five, was violated.

Fisher's exact test can only be used on 2 x 2 contingency tables, as a result two sets of contingency tables were prepared, the first set used presence / absence (0-1) data and the second set used low / high intensity (1-2) data (Table 7.2). A low intensity infection of *P. laevis* was when one to ten worms occurred in a fish and a high intensity infection was when eleven or more worms occurred in a fish. A low intensity infection of *A. clavula* was when one to twenty-five worms occurred in a fish and a high intensity infection was when twenty-six or more worms occurred in a fish.

Percentage of column totals showed that in 54.2% of cases when *P. laevis* was absent, *A. clavula* was also absent. In 45.8% of cases *P. laevis* was present when *A. clavula* was absent. When the percentage of column totals were examined for the low / high intensity contingency tables, *P. laevis* and *A. clavula* were present together in 100% of low intensity infections. In all cases when *A. clavula* occurred at high intensity when *P. laevis* occurred at low intensity, and in no case did *P. laevis* occur at high intensity when *A. clavula* occurred at low intensity. Fisher's exact test showed a significant relationship between the presence / absence of *P. laevis* and *A. clavula*, however for the low, high intensity contingency table there was no significant relationship between *P. laevis* and *A. clavula*.

Three-way analysis of variance was used to examine the relationship between month, infection status (whether *P. laevis* were present in single or concurrent infections), infection intensity (low, medium, high) and the total number of *P. laevis* worms recorded. Significant differences existed in the number of *P. laevis* recorded in low, medium and high intensity infections (F ratio = 416.5; df = 2,1689; $p \leq 0.0001$). Significant differences also existed in the number of *P. laevis* recorded between months (F ratio = 49.3; df = 3,1689; $p \leq 0.0001$), however no significant differences

existed in the number of *P. laevis* recorded in single or concurrent infections. The interaction between infection intensity and month was significant (F ratio = 55.8; df = 6,1689; $p \leq 0.0001$) as was the interaction between infection intensity and infection status (F ratio = 3.5; df = 2,1689; $p = 0.03$). The interaction between month and infection status was significant (F ratio = 21.1; df = 3,1689; $p \leq 0.0001$) and the interaction between infection status, month and infection intensity was also significant (F ratio = 24.2; df = 6,1689; $p \leq 0.0001$).

Table 7.1 Statistics summarising the mean number of *P. laevis* worms for each month and for the total sample when *P. laevis* co-occurred with *A. clavula* and occurred alone in Lough Feeagh.

	April	May	August	November	Total
<i>P. laevis</i>					
Count	181	368	283	487	1319
Mean ($\pm$ S.D.)	4.76(5.03)	11(13.9)	6.76(7.1)	11(11.25)	8.46(10.28)
Minimum	1	1	1	1	1
Maximum	24	80	29	42	80
Range	23	79	28	41	79
<i>P. laevis</i> & <i>A. clavula</i>					
Count	82	120	56	143	401
Mean ($\pm$ S.D.)	4.24(5.48)	6.05(4.99)	3.05(2.8)	6(10.92)	5.01(7.1)
Minimum	1	1	1	1	1
Maximum	39	56	32	44	56
Range	38	55	31	43	55

Table 7.2 Presence / absence and low / high contingency table for the total sample of *P. laevis* / *A. clavula* in trout in Lough Feeagh (*n* = 379).

Row Totals = *P. laevis*

Column Totals = *A. clavula*

Presence / Absence				Low / High Intensity			
	0	1	Total		1	2	Total
0	143	0	143	1	104	11	115
	100	0	100		90.4	9.6	100
	54.2	0	37.7		100	100	100
	37.7	0	37.7		90.4	9.6	100
1	121	155	236	2	0	0	0
	51.3	48.7	100		0	0	100
	45.8	100	62.3		0	0	0
	31.9	30.3	62.3		0	0	0
Total	264	115	379	Total	104	11	115
	69.7	30.3	100		90.4	9.6	100
	100	100	100		100	100	100
	69.7	30.3	100		90.4	9.6	100

Count

% of Row Total

% of Column Total

% of Table Total

Fishers Exact Test < 0.0001

Fishers Exact Test = 1.00

7.3 Comparison of the size of *P. laevis* in single and concurrent infections with *A. clavula* in the total trout sample and in each sample month

Length

The mean length of the total sample of *P. laevis* when it occurred alone was 8.49mm (± 2.7) (Table 7.3). The mean lengths of *P. laevis* increased from April to a peak in August and subsequently decreased in November (Table 7.4; Fig 7.1). The mean length of the total sample of *P. laevis* co-occurring with *A. clavula* was 8.46mm(± 3.04) (Table 7.4). The mean lengths of *P. laevis* co-occurring with *A. clavula* decreased from April to the lowest value in May, increased to a peak in August and decreased again November (Table 7.4; Fig 7.1).

Weight

The mean weight of the total sample of *P. laevis* when it occurred alone was 4.47mg(± 4.65)(Table 7.3). The mean weights of *P. laevis* increased from April to a peak in August and then decreased substantially in November (Table 7.3; Fig 7.1). The mean weight of the total sample of *P. laevis* co-occurring with *A. clavula* was 4.94mg(± 6.34) (Table 7.4). The mean weights of *P. laevis* decreased from April to May, increased to a peak in August and subsequently decreased to their lowest level in November (Table 7.4; Fig 7.1).

Two-way analysis of variance was used to examine the relationship between month, infection status of *P. laevis* (whether worms were present as single or concurrent infections) and the length of *P. laevis* worms present. A significant difference existed in the length of *P. laevis* recorded in each month (F ratio = 122.4; df = 3,1712; $p \leq 0.0001$). A significant difference also existed in the length of *P. laevis* recorded between single and concurrent infections (F ratio = 8.5; df = 1,1712; $p \leq 0.004$). The mean length of *P. laevis* was longer in concurrent infections in April, August and November but longer in single species infections in May and for the total sample.

Finally the interaction between the month and the infection status of *P. laevis* was also significant (F ratio = 5.0; df = 3,1712; $p \leq 0.002$). Month was the most significant factor in this two-way analysis

Two-way analysis of variance was also used to examine the relationship between month, infection status of *P. laevis* (whether worms were present as single or concurrent infections) and the log (x+1) transformed weights of *P. laevis* worms present. A significant difference existed in the weight of *P. laevis* recorded in each month (F ratio = 162.9; df = 3,1708; $p \leq 0.0001$). A significant difference also existed in the weight of *P. laevis* recorded between single and concurrent infections (F ratio = 5.8; df = 1,1708; $p = 0.017$). The mean weight of *P. laevis* was greater in concurrent infections in April, August and November and for the total sample, but greater for single species infections in May. Finally the interaction between the month and the infection status of *P. laevis* was also significant (F ratio = 7.5; df = 3,1708; $p \leq 0.001$). Month was also the most significant factor in this two-way analysis.

Table 7.3 Statistics summarising the length distributions (in mm) and weight distributions (in mg) of *P. laevis* occurring alone in Lough Feeagh, for the total sample and for each sample month.

	April	May	August	November	Total
Length					
Count	181	368	283	487	1319
Mean ($\pm$ S.D.)	6.98(1.85)	7.86(2.32)	11.02(2.82)	8.06(2.17)	8.49(2.7)
Minimum	2	2	2	3	2
Maximum	13	16	21	18	21
Range	11	14	19	15	19
Weight					
Count	181	368	281	486	1316
Mean ($\pm$ S.D.)	3.5(2.42)	3.84(3.03)	8.53(6.09)	2.97(3.96)	4.47(4.65)
Minimum	1	0.5	1	***	***
Maximum	18	39	51	40	51
Range	17	38.5	50	40	51

*** = The minimum weight was smaller than the lowest value recorded by the balance.

Table 7.4 Statistics summarising the length distributions (in mm) and weight distributions (in mg) of *P. laevis* co-occurring with *A. clavula* in Lough Feeagh, for the total sample and for each sample month.

	April	May	August	November	Total
Length					
Count	82	120	56	143	401
Mean ($\pm$ S.D.)	8.05(2.67)	7.59(2.67)	11.91(3.48)	8.07(2.39)	8.46(3.04)
Minimum	3	1	3	3	1
Maximum	14	14	20	20	20
Range	11	13	17	17	19
Weight					
Count	82	120	56	143	401
Mean ($\pm$ S.D.)	5.13(4.11)	3.43(2.19)	12.32(9.67)	3(6.06)	4.94(6.34)
Minimum	1	0.5	1	0.5	0.5
Maximum	20	10	41	40	41
Range	19	9.5	40	39.5	40.5

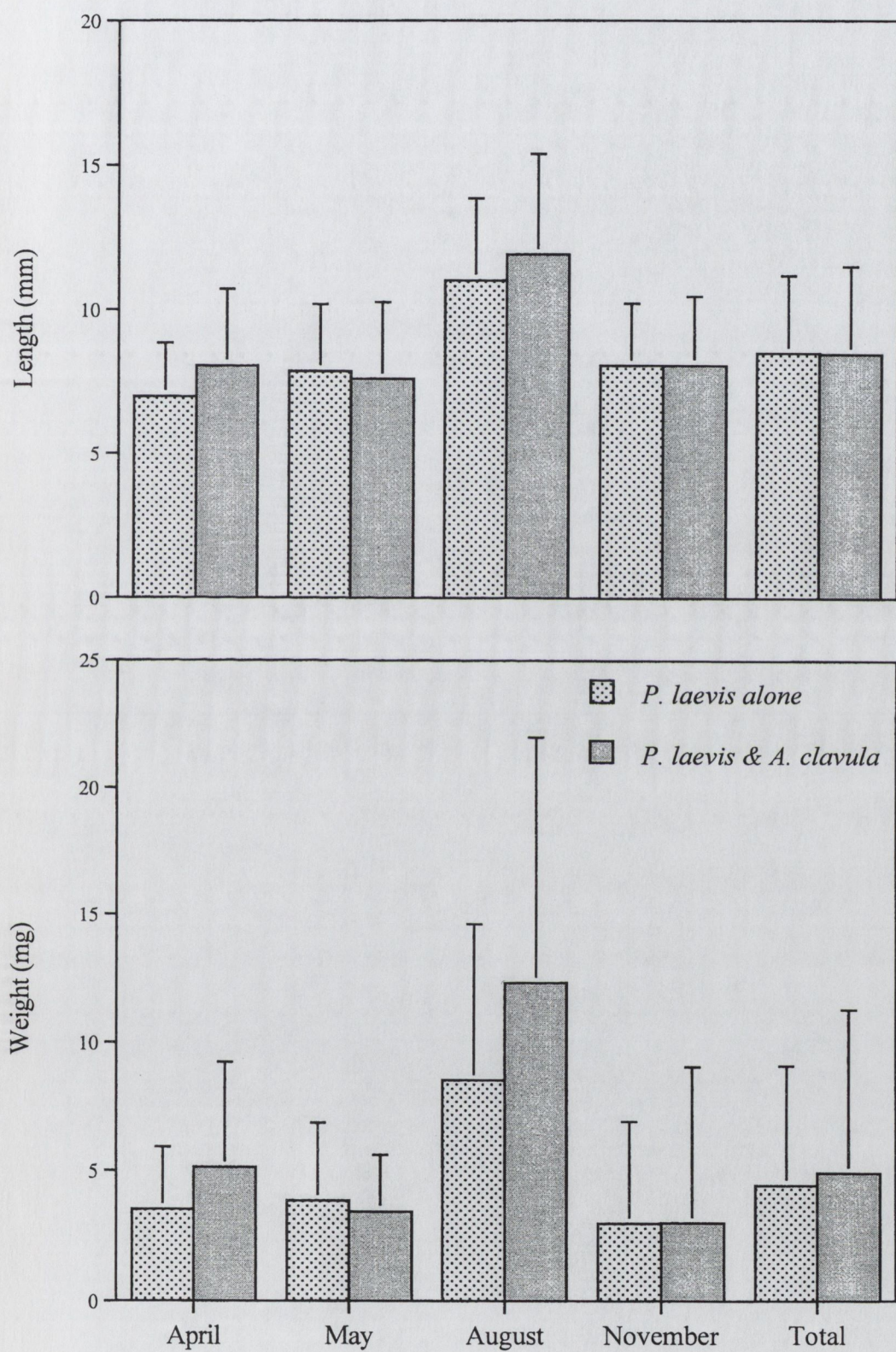


Fig 7.1 Mean lengths and weights (+ S.D.) of *P. laevis* in single and concurrent infections with *A. clavula* in trout in Lough Feeagh for the total sample and for each sample month.

7.4 Comparison of the size of *P. laevis* in single and concurrent infections with *A. clavula* in low, medium and high intensity infections

Length

The mean length values for *P. laevis* occurring alone decreased from 9.17mm(± 3.17) in low intensity infections to 7.99mm(± 2.52) in medium intensity infections and 8.39mm(± 2.55) in high intensity infections (Table 7.5; Fig 7.2). The mean length values for *P. laevis* co-occurring with *A. clavula* decreased from 9.52mm(± 3.47) in low intensity infections to 7.73mm(± 2.29) in medium intensity infections and subsequently increased to 7.93mm(± 2.72) in high intensity infections (Table 7.5; Fig 7.2).

Weight

The mean weight values for *P. laevis* occurring alone decreased substantially from 6.83mg(± 6.87) in low intensity infections to 3.84mg(± 3.6) in medium intensity infections and subsequently increased to 3.94mg(± 3.78) in high intensity infections (Table 7.5; Fig 7.2). The mean weight values for *P. laevis* co-occurring with *A. clavula* decreased substantially from 7.24mg(± 8.43) in low intensity infections to 3.27mg(± 3.24) in medium intensity infections and 3.83mg(± 4.68) in high intensity infections (Table 7.5; Fig 7.2).

Two-way analysis of variance was used to examine the relationship between infection intensity (whether worms were in low, medium or high intensity infections), infection status (whether worms were present as single or concurrent infections) and the length of *P. laevis* worms present. A significant difference existed in the lengths of *P. laevis* recorded in low, medium and high intensity infections (F ratio = 28.2; df = 2,1715; $p \leq 0.0001$). However no significant differences existed in the length of *P. laevis* recorded between single and concurrent infections or the interactions between the infection intensity and the infection status.

Two-way analysis of variance was also used to examine the relationship between infection intensity (whether worms were in low, medium or high intensity infections), infection status (whether worms were present as single or concurrent infections) and the $\log (x+1)$ transformed weights of *P. laevis* worms present. A significant difference existed in the weights of *P. laevis* recorded low, medium and high intensity infections (F ratio = 53.6; df = 2,1710; $p \leq 0.0001$). A significant difference also existed in the weight of *P. laevis* recorded between single and concurrent infections (F ratio = 4.9; df = 1,1710; $p = 0.027$). The interaction between the infection intensity and the infection status of *P. laevis* was not significant.

Table 7.5 Statistics summarising the length and weight distributions (in mm and mg respectively) of low, medium and high intensity infections of *P. laevis* co-occurring with *A. clavula* and *P. laevis* occurring alone in Lough Feeagh.

<i>P. laevis</i>	Low		Medium		High	
	Length	Weight	Length	Weight	Length	Weight
Count	251	250	157	157	911	909
Mean ($\pm$ S.D.)	9.17(3.17)	6.83(6.87)	7.99(2.52)	3.84(3.6)	8.39(2.55)	3.94(3.78)
Minimum	3	0.5	2	0.5	2	***
Maximum	21	51	16	24	18	31
Range	18	50.5	14	23.5	16	31
<i>P. laevis</i> & <i>A. clavula</i>						
Count	145	145	84	84	172	172
Mean ($\pm$ S.D.)	9.52(3.47)	7.24(8.43)	7.73(2.29)	3.27(3.24)	7.93(2.72)	3.83(4.68)
Minimum	3	0.5	3	0.5	1	0.5
Maximum	20	41	14	15	19	38
Range	17	40.5	11	14.5	18	37.5

*** = The minimum weight was smaller than the lowest value recorded by the balance.

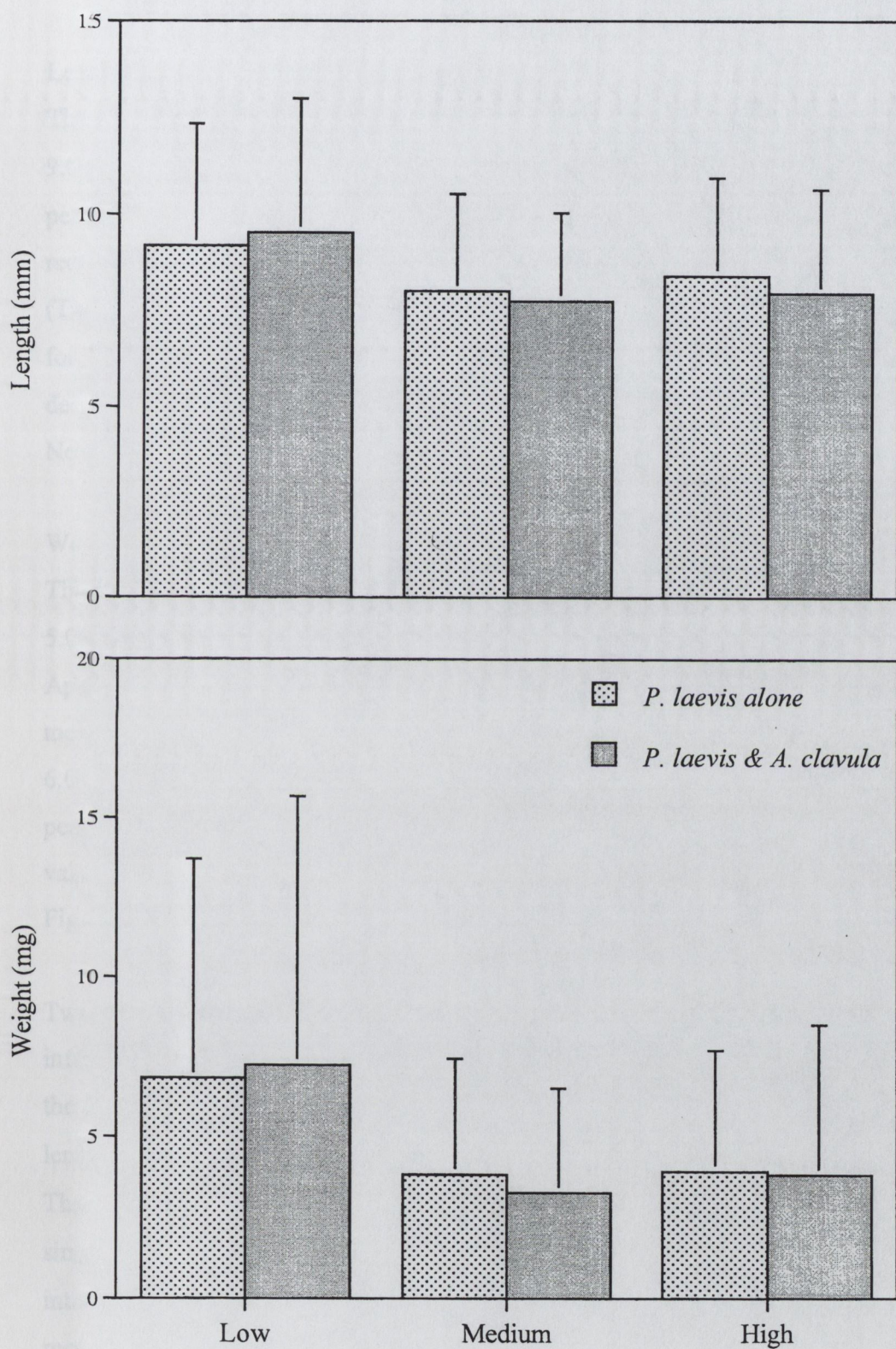


Fig 7.2 Mean lengths and weights (+ S.D.) of low, medium and high intensity infections of *P. laevis* when it occurred in single and concurrent infections with *A. clavula* in trout in Lough Feeagh.

7.5 Comparison of the size of female *P. laevis* in single and concurrent infections of *A. clavula* in the total trout sample and in each sample month

Length

The mean length value for the total sample of female *P. laevis* occurring alone was 9.01mm(± 2.74) (Table 7.6; Fig 7.3). Mean length values increased from April to a peak in August and subsequently decreased in November. The mean length value recorded in November was comparable to the value recorded for the total sample (Table 7.6; Fig 7.3). The mean length of female *P. laevis* co-occurring with *A. clavula* for the total sample was 9.4mm(± 3.24) (Table 7.7; Fig 7.3). Mean length values decreased from April to May, increased to a peak in August and decreased again in November (Table 7.7; Fig 7.3).

Weight

The mean weight value for the total sample of female *P. laevis* occurring alone was 5.09mg(± 5.09) (Table 7.7; Fig 7.3). Mean weight values increased substantially from April to a peak in August and then decreased in November (Table 7.6; Fig 7.3). The mean weight for the total sample of *P. laevis* co-occurring with *A. clavula* was 6.04mg(± 7.41) (Table 7.7; Fig 7.3). Mean weight values decreased from April to May peaked in August and then decreased substantially in November. The mean weight value for the total sample was comparable to the value recorded in April (Table 7.7; Fig 7.3).

Two-way analysis of variance was used to examine the relationship between month, infection status (whether worms were present as single or concurrent infections) and the length of female *P. laevis* worms present. A significant difference existed in the lengths of female *P. laevis* between month (F ratio = 75.3; df = 3,850; $p \leq 0.0001$). There was also a significant difference in the length of female *P. laevis* between single and concurrent infections (F ratio = 10.6; df = 1,850; $p \leq 0.001$), however the interaction between month and infection status was not significant. Month was the most significant factor in this two-way analysis.

Two-way analysis of variance was also used to examine the relationship between month, infection status (whether worms were present as single or concurrent infections) and the log (x+1) transformed weights of female *P. laevis* worm. A significant difference existed in the log (x+1) transformed weights of female *P. laevis* between months (F ratio = 83.8; df = 3,849; $p \leq 0.0001$). There was no significant difference in the log (x+1) transformed weights of female *P. laevis* between single and concurrent infections, however the interaction between season and infection status was significant (F ratio = 3.2; df = 3,849; $p = 0.02$). Month was also the most significant factor in this two-way analysis.

Table 7.6 Statistics summarising the length distributions (in mm) and weight distributions (in mg) of female *P. laevis* occurring alone in Lough Feeagh, for the total sample and for each sample month.

	April	May	August	November	Total
Length					
Count	100	189	142	244	675
Mean ($\pm$ S.D.)	7.5(1.74)	8.28(2.26)	11.85(2.57)	8.56(2.34)	9.01(2.74)
Minimum	3	4	2	3	2
Maximum	13	16	18	18	18
Range	10	12	16	15	16
Weight					
Count	100	189	142	244	675
Mean ($\pm$ S.D.)	3.95(2.63)	4.17(3.3)	9.95(6.15)	3.44(4.59)	5.09(5.09)
Minimum	1	0.5	1	***	***
Maximum	18	39	33	40	40
Range	17	38.5	32	40	40

*** = The minimum weight was smaller than the lowest value recorded by the balance.

Table 7.7 Statistics summarising the length distributions (in mm) and weight distributions (in mg) of female *P. laevis* co-occurring with *A. clavula* in Lough Feeagh, for the total sample and for each sample month.

	April	May	August	November	Total
Length					
Count	46	43	31	63	183
Mean ($\pm$ S.D.)	8.69(2.71)	8.56(2.99)	12.9(3.21)	8.75(2.65)	9.4(3.24)
Minimum	4	3	8	3	3
Maximum	14	14	20	20	20
Range	10	11	12	17	17
Weight					
Count	46	43	31	63	183
Mean ($\pm$ S.D.)	6.07(4.79)	3.84(2.21)	13.54(10.43)	3.84(7.22)	6.04(7.41)
Minimum	1	0.5	2	1	0.5
Maximum	20	10	41	40	41
Range	19	9.5	39	39	40.5

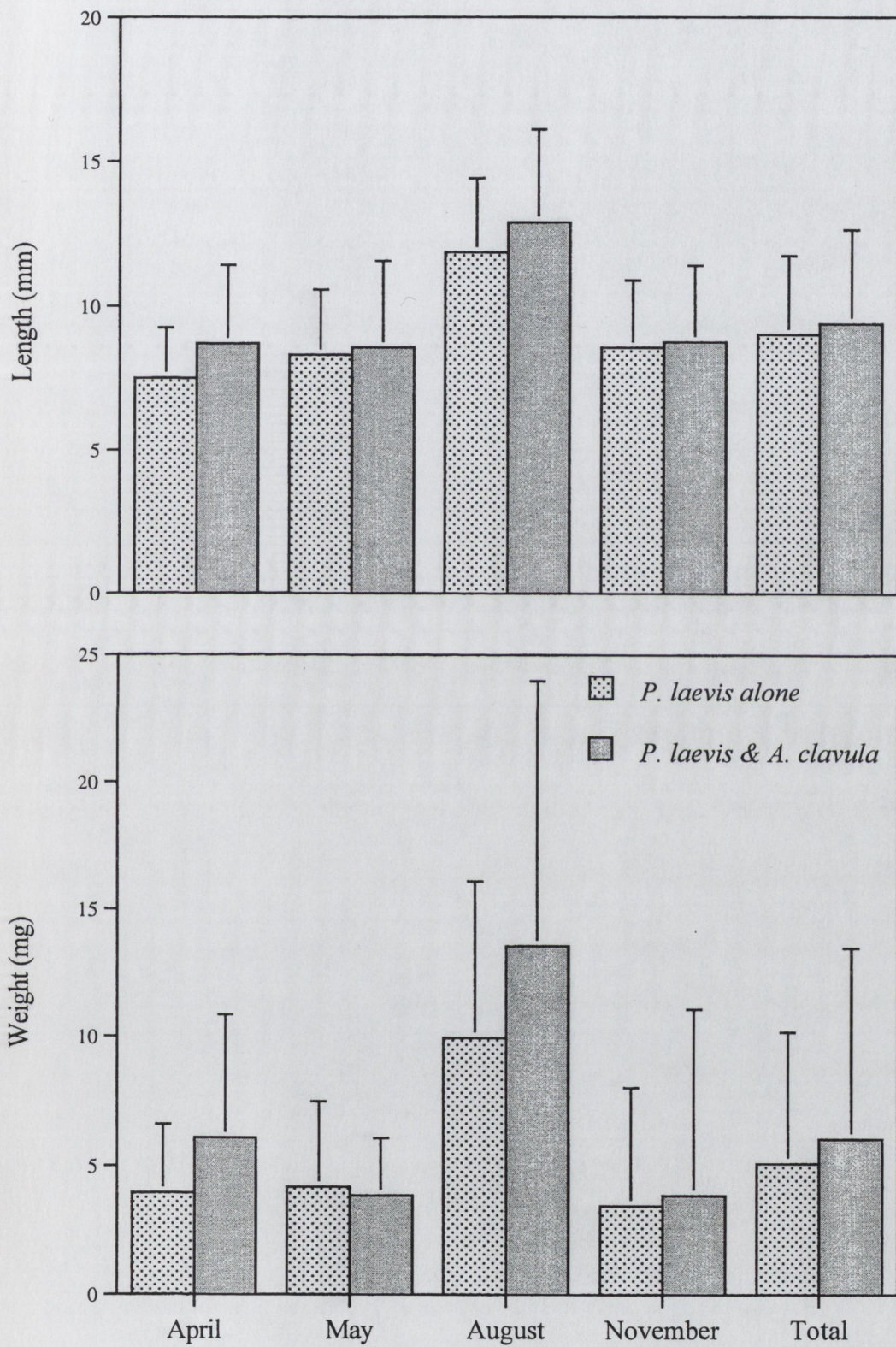


Fig 7.3 Mean lengths and weights (+ S.D.) of female *P. laevis* in single and concurrent infections with *A. clavula* in trout in Lough Feeagh for the total sample and for each sample month.

7.6 Comparison of the size of stage I, II and III female *P. laevis* in single and concurrent infections with *A. clavula*

In single species infections of *P. laevis* 62% (368 worms) were of stage I maturity, 16% (96 worms) were of stage II maturity and 22% (129 worms) of worms were of stage III maturity. In concurrent infections of *P. laevis* and *A. clavula* 76% (113 worms) were of stage I maturity, 11% (17 worms) were of stage II maturity and 13% (19 worms) were of stage III maturity. Chi-squared tables were used to compare the proportions of stage I, II and III female *P. laevis* in single and concurrent infections with *A. clavula* (Table 7.8). Significantly more stage I, II and III female *P. laevis* were found in single infections (Chi-square = 10.11; $p \leq 0.006$).

Length of stage I, II and III female *P. laevis*

The mean length of *P. laevis* occurring alone increased from 7.96mm(± 2.2) in stage I females to 8.34mm(± 2.07) in stage II females and then increased to a peak of 11.92mm(± 2.59) in stage III females (Table 7.9; Fig 7.4). The mean length of *P. laevis* co-occurring with *A. clavula* decreased from 8.53mm(± 2.81) in stage I females to 8.48mm(± 2.6) in stage II females and then increased to 12.65mm(± 3.46) in stage III females (Table 7.9; Fig 7.4).

Weight of stage I, II and III female *P. laevis*

The mean weight of *P. laevis* occurring alone increased from 3.21mg(± 2.68) for stage I females, to 4.26mg(± 2.54) for stage II females and peaked at 10.62mg(± 7.46) for stage III females (Table 7.9; Fig 7.4). The mean weight of *P. laevis* co-occurring with *A. clavula* increased from 4.38mg(± 5.82) for stage I females, to 5.35mg(± 4.25) for stage II females and peaked at 12.65mg(± 3.46) for stage III females (Table 7.9; Fig 7.4).

Two-way analysis of variance was used to examine the relationship between maturity status (stage I, II or III female), infection status (whether worms were present as

single or concurrent infections) and the length of female *P. laevis* worms present. A significant difference existed in the lengths of *P. laevis* between stage I, II and III females (F ratio = 55.4; df = 2,736; $p \leq 0.0001$). No significant differences existed in the lengths of *P. laevis* recorded between single and concurrent infections or for the interaction between maturity status and infection status.

Two-way analysis of variance was also used to examine the relationship between maturity status (stage I, II or III female), infection status (whether worms were present as single or concurrent infections) and the log (x+1) transformed weights of *P. laevis* worms present. A significant difference existed in the weights of *P. laevis* between stage I, II and III females (F ratio = 57.5; df = 2,735; $p \leq 0.0001$). No significant differences existed in the weights of *P. laevis* recorded between single and concurrent infections or for the interaction between maturity status and infection status.

Table 7.8 Contingency table comparing the proportions of stage I, II and III female *P. laevis* in single and concurrent infections with *A. clavula*.

Row Totals = Presence or absence of *A. clavula*
 Column Totals = Maturity status of female *P. laevis*

	Stage I	Stage II	Stage III	Total
0	368	96	129	593
	62.1	16.2	21.8	100
	76.5	85	87.2	79.9
	49.6	12.9	17.4	79.9
1	113	17	19	149
	75.8	11.4	12.8	100
	23.5	15	12.8	20.1
	15.2	2.29	2.56	20.1
Total	481	113	148	742
	64.8	15.2	19.9	100
	100	100	100	100
	64.8	15.2	19.9	100
Count				
% of Row Total				
% of Column Total				
% of Table Total				
Chi - square = 10.11; df = 2; p < 0.006				

Table 7.9 Statistics summarising the length and weight distributions (in mm and mg respectively) of stage I, II and III female *P. laevis* co-occurring with *A. clavula* and *P. laevis* occurring alone in Lough Feeagh.

<i>P. laevis</i>	Stage I		Stage II		Stage III	
	Length	Weight	Length	Weight	Length	Weight
Count	368	368	96	96	129	129
Mean ($\pm$ S.D.)	7.96(2.2)	3.21(2.68)	8.34(2.07)	4.26(2.54)	11.92(2.59)	10.62(7.46)
Minimum	2	***	4	1	5	1
Maximum	15	24	15	16	18	40
Range	13	24	11	15	13	39
<i>P. laevis</i> & <i>A. clavula</i>						
Count	113	113	17	17	19	19
Mean ($\pm$ S.D.)	8.53(2.81)	4.38(5.82)	8.48(2.6)	5.35(4.25)	12.65(3.46)	14.42(12.6)
Minimum	3	0.5	4	1	8	2
Maximum	20	41	13	16	20	40
Range	17	40.5	9	15	12	38

*** = The minimum weight was smaller than the lowest value recorded by the balance.

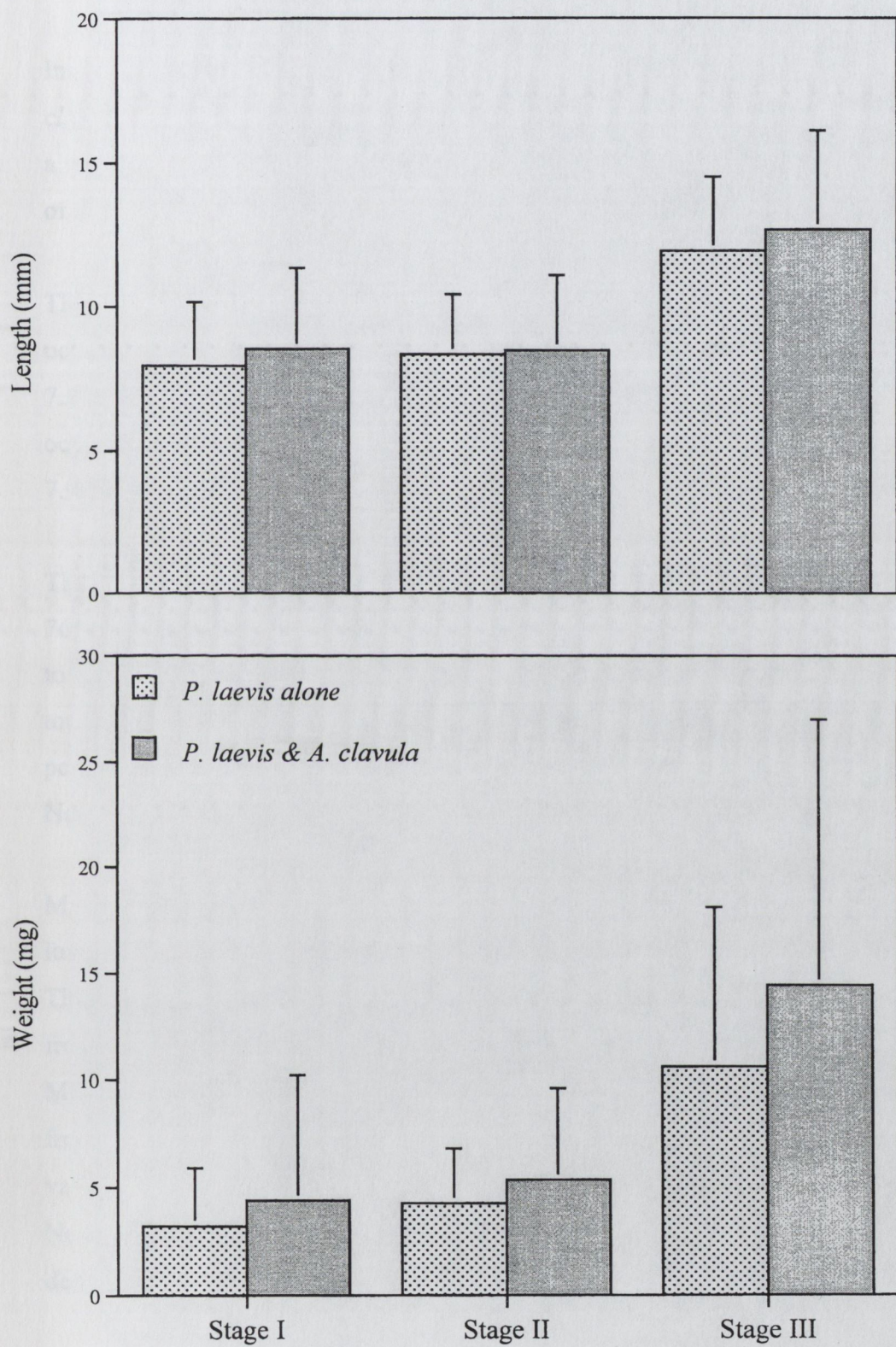


Fig 7.4 Mean lengths and weights (+ S.D.) of stage I, II and III female *P. laevis* in single and concurrent infections with *A. clavula* in trout in Lough Feeagh.

7.7 Comparison of the niches of *P. laevis* co-occurring with *A. clavula* in trout in each sample month and in the total sample

In this section the niches of *P. laevis* were examined when it co-occurred with *A. clavula* and when it occurred alone in each sample month and for the total sample. In a manner similar to previous chapters a set of statistics summarising the distribution of *P. laevis* along the intestine have been provided.

The fundamental niches of *P. laevis* co-occurring with *A. clavula* and *P. laevis* occurring alone in the intestine of trout from Lough Feeagh were first examined (Fig 7.5). The distributions of *P. laevis* co-occurring with *A. clavula* and *P. laevis* occurring alone in the intestine were then examined for each sample month (Figs 7.6-7.9).

The mean percentage location for the total sample of *P. laevis* occurring alone was 76.82% (Table 7.10). Mean percentage locations also decreased from a peak in April to the lowest value in November (Table 7.10). The mean percentage location for the total sample of *P. laevis* co-occurring with *A. clavula* was 77.15% (Table 7.11). Mean percentage location values decreased from a peak in April to the lowest value in November. Mean location values for May and August were comparable.

Minimum values for *P. laevis* occurring alone decreased from a peak in April to the lowest value in November. Maximum values were 100% in all months (Table 7.10). Thus the range of occurrence of *P. laevis* occurring alone in Lough Feeagh increased from the lowest value in April to a peak in November (Table 7.10; Figs 7.6-7.9). Minimum values for *P. laevis* co-occurring with *A. clavula* decreased substantially from April to May, increased in August and decreased again in November. Maximum values were 100% in April and May and 98.86% and 98.75% in August and November respectively. Thus the range of occurrence increased from April to May, decreased in August and increased again in November (Table 7.11; Figs 7.6-7.9).

25% and 75% values for *P. laevis* occurring alone in Lough Feeagh decreased from a peak in April to the lowest values in November (Table 7.10). However the interquartile range increased from the lowest value in April to a peak in November (Table 7.10). 25% and 75% quartile values for *P. laevis* co-occurring with *A. clavula* decreased from April to May, increased in August and decreased again in November (Table 7.11). Thus the interquartile range increased from April to May, decreased in August and increased again in November (Table 7.11).

Skewness values for *P. laevis* occurring alone were negative and below one in April, May and November and positive and below one in August. Kurtosis values were positive in all months. Thus the distributions of *P. laevis* occurring alone in Lough Feeagh were peaked but approximated normal in all months (Table 7.10; Figs 7.6-7.9). Skewness values for *P. laevis* co-occurring with *A. clavula* were negative and below one in April, August and November and negative and greater than one in May. Kurtosis values were positive in all months. Thus the distributions of *P. laevis* co-occurring with *A. clavula* were peaked but approximated normal in the April, August and November samples and peaked and negatively skewed in the May sample (Table 7.11; Figs 7.6-7.9).

Two-way analysis of variance was used to examine the relationship between month, infection status of *P. laevis* (whether worms were present as single or concurrent infections) and the percentage position of *P. laevis* worms present. A significant difference existed in the percentage positions of *P. laevis* recorded in each month (F ratio = 57.6; $df = 3,1707$; $p \leq 0.0001$). No significant difference existed in the percentage position of *P. laevis* recorded in single and concurrent infections. However the interaction between the month and the infection status of *P. laevis* was significant (F ratio = 5.9; $df = 3,1707$; $p \leq 0.0005$).

In a similar manner to previous chapters the niche width of *P. laevis* in single and concurrent infections in the intestine of wild trout from Lough Feeagh was calculated using Culver's 1972 standardised Shannon-Wiener function, H' . The niche width of

the total sample of *P. laevis* in single species infections was 0.78. Niche width values increased from 0.69 in April to 0.7 in May, decreased to 0.66 in August and increased again to 0.78 in November. The niche width of the total sample of *P. laevis* in concurrent infections with *A. clavula* was 0.76. Niche width values increased from 0.67 in April to 0.72 in May, decreased to 0.69 in August and subsequently increased to 0.75 in November.

Niche overlaps were calculated for *P. laevis* and *A. clavula* in concurrent infections in Lough Feeagh using the Morisita-Horn measure (Magurran, 1998). The niche overlap value for the total sample was 0.74. Niche overlap values decreased from 0.48 in April to 0.33 in May, and increased to 0.4 in August and 0.44 in November.

Table 7.10 Statistics summarising the distributions of *P. laevis* occurring alone in Lough Feeagh, for the total sample and for each sample month.

	April	May	August	November	Total
Count	182	367	282	488	1319
Mean ($\pm$ S.D.)	82.87(8.5)	81.65(9.98)	77.12(8.1)	70.93(11.53)	76.82(11.48)
Median	83.5	80.2	76.1	71.27	76.65
Inter quartile	11.2	11.42	12.6	12.89	13.28
Range					
Minimum	47.2	37.5	35.5	31.49	31.49
Maximum	100	100	100	100	100
Range	52.8	62.5	64.5	68.51	68.51
Skewness	-0.45	-0.79	0.04	-0.28	-0.8
Kurtosis	1.19	2.54	2.22	0.76	2.72
Lower (25%)	77	76.61	70.7	64.11	70.7
Upper (75%)	88.2	88.03	83.3	77	83.98

Table 7.11 Statistics summarising the distributions of *P. laevis* co-occurring with *A. clavula* in Lough Feeagh, for the total sample and for each sample month.

	April	May	August	November	Total
Count	82	120	56	143	401
Mean ($\pm$ S.D.)	82.24(9.17)	77.59(13.93)	78.65(9.78)	73.29(11.29)	77.15(12)
Median	81.9	77.75	79.15	73.91	77.02
Inter quartile	13.19	13.7	10.36	13.12	12.68
Range					
Minimum	48.33	26.6	43.48	37.14	26.6
Maximum	100	100	98.86	98.85	100
Range	51.67	73.4	55.38	61.71	73.4
Skewness	-0.06	-1.14	-0.69	-0.64	-0.84
Kurtosis	1.08	2.54	1.76	1.37	2.21
Lower (25%)	75.51	71	74.4	67.42	71.42
Upper (75%)	88.7	84.7	85.36	80.54	84.1

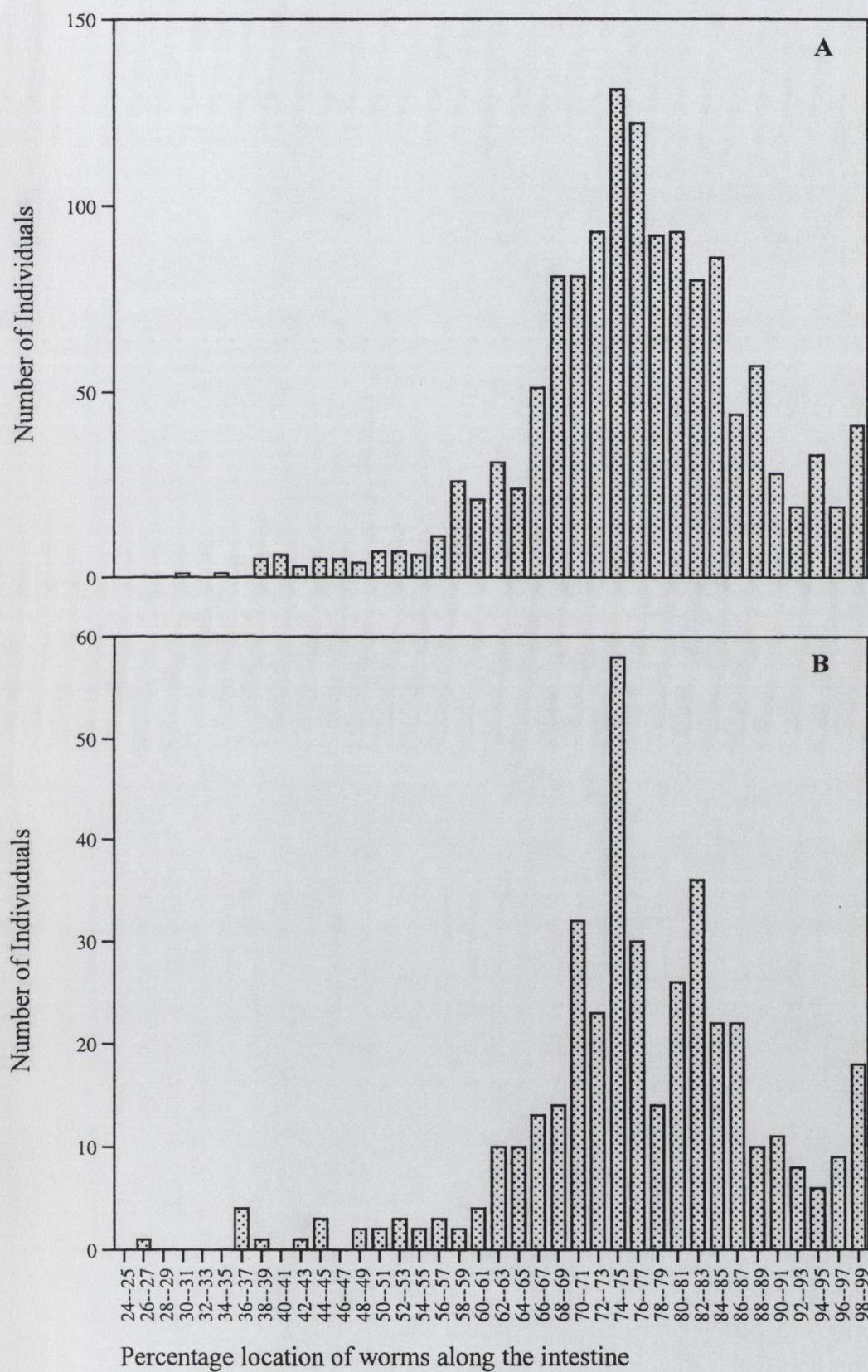


Fig 7.5 Niche for the total sample of *P. laevis* when occurred alone (A) and when it co-occurred with *A. clavula* (B) in trout in Lough Feeagh.

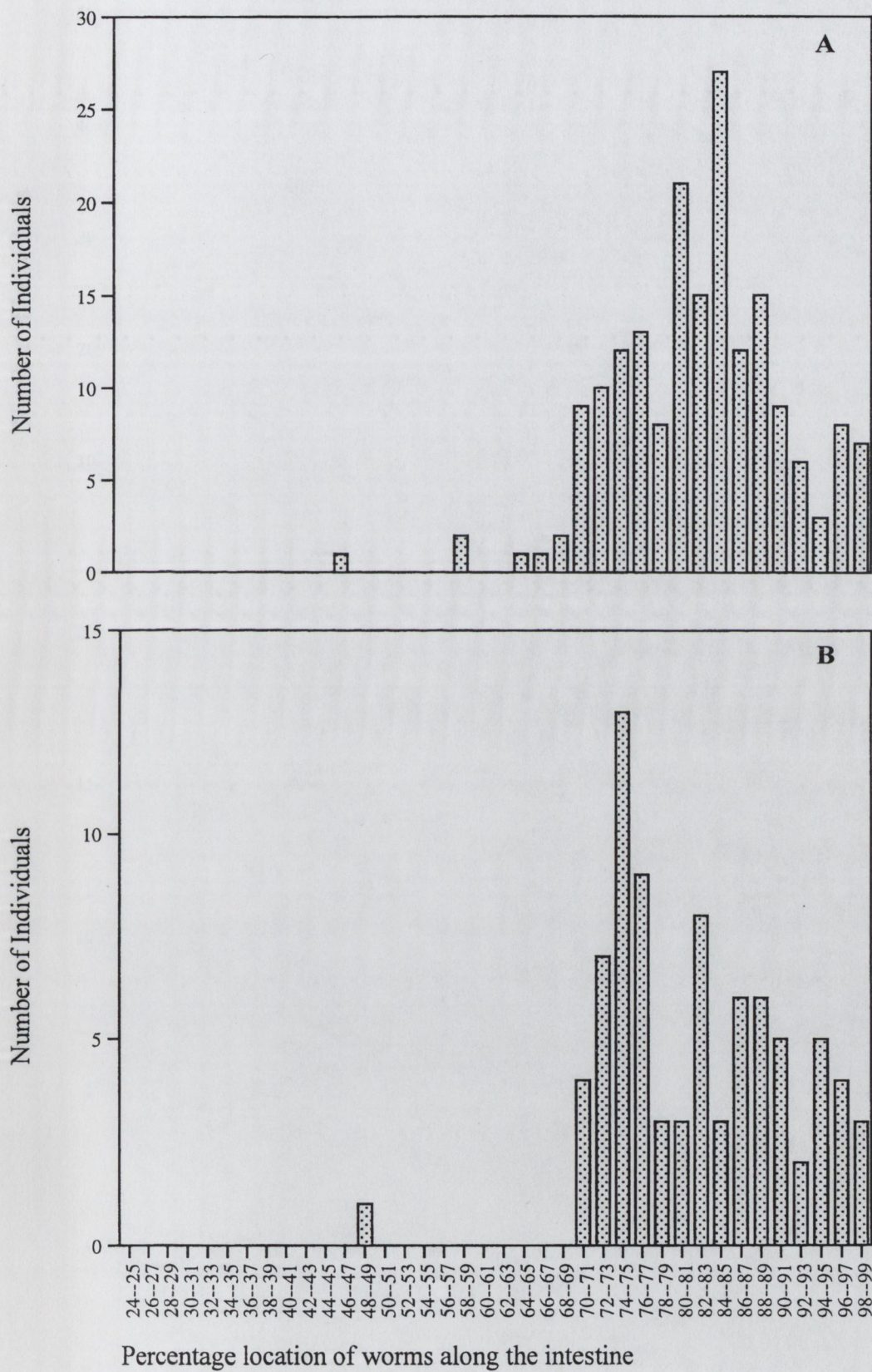


Fig 7.6 Niches for *P. laevis* when it occurred alone (A) and when it co-occurred with *A. clavula* (B) in Lough Feeagh, in April.

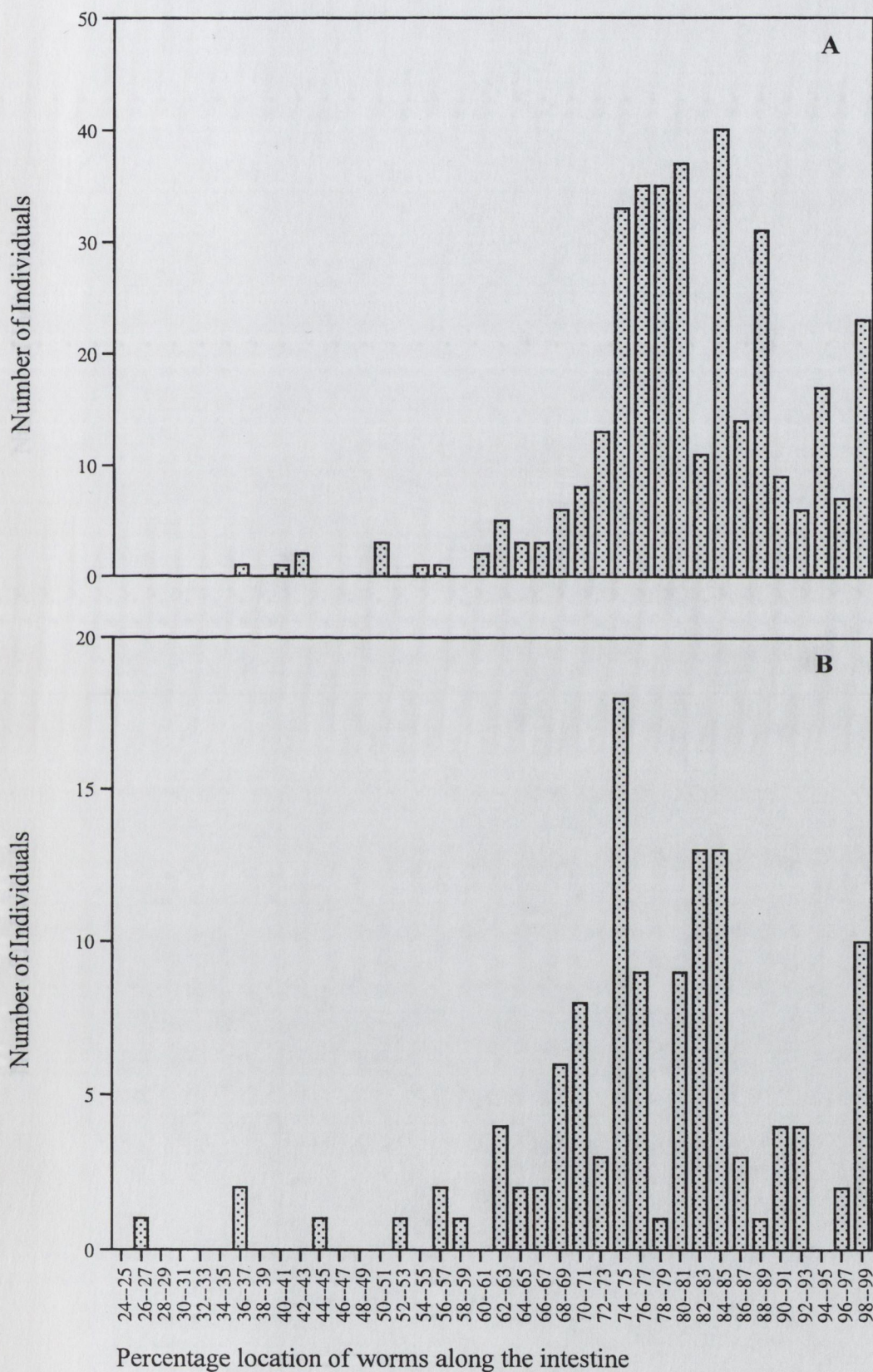


Fig 7.7 Niches for *P. laevis* when it occurred alone (A) and when it co-occurred with *A. clavula* (B) in Lough Feeagh, in May.

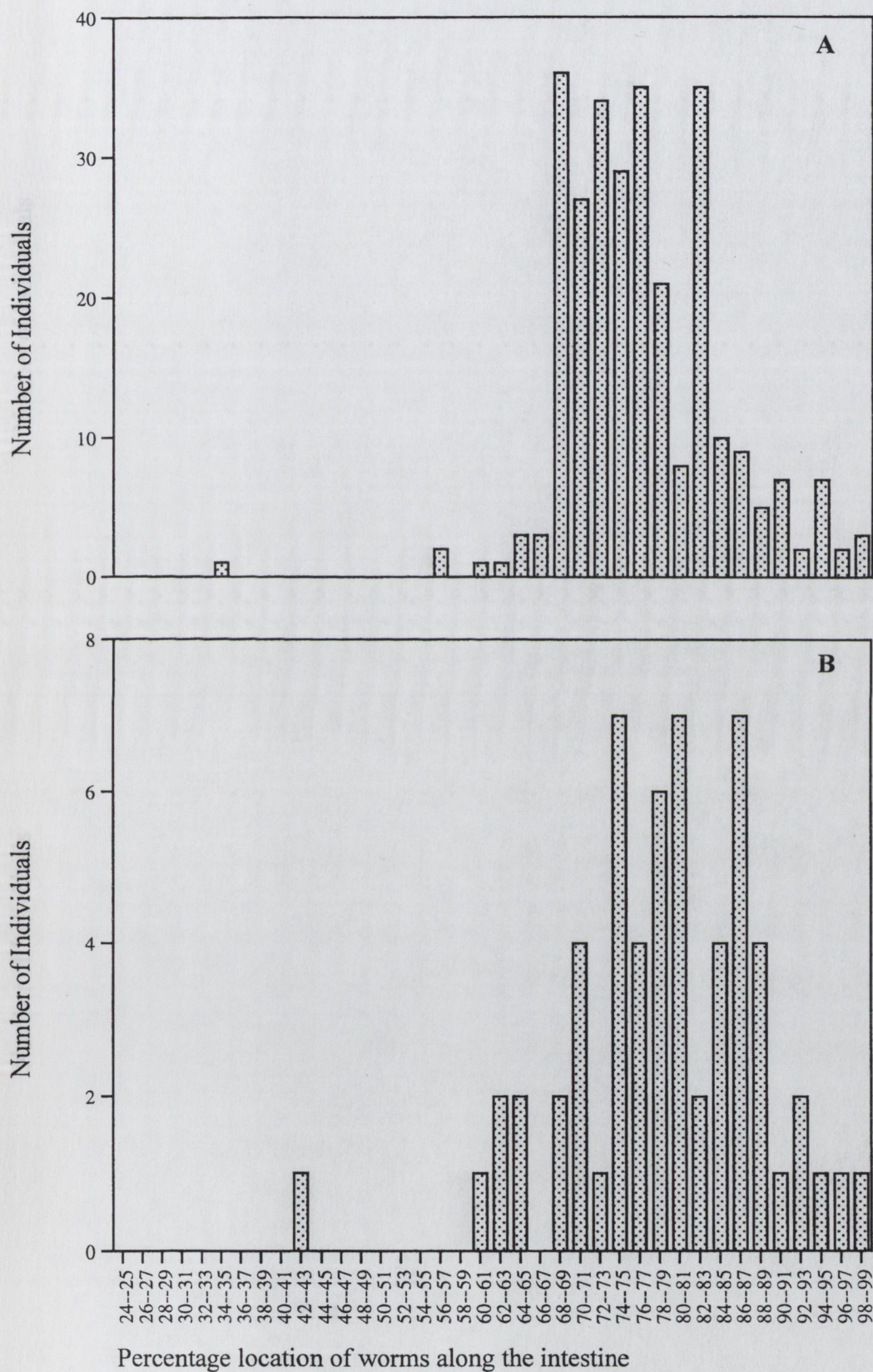


Fig 7.8 Niches for *P. laevis* when it occurred alone (A) and when it co-occurred with *A. clavula* (B) in Lough Feeagh, in August.

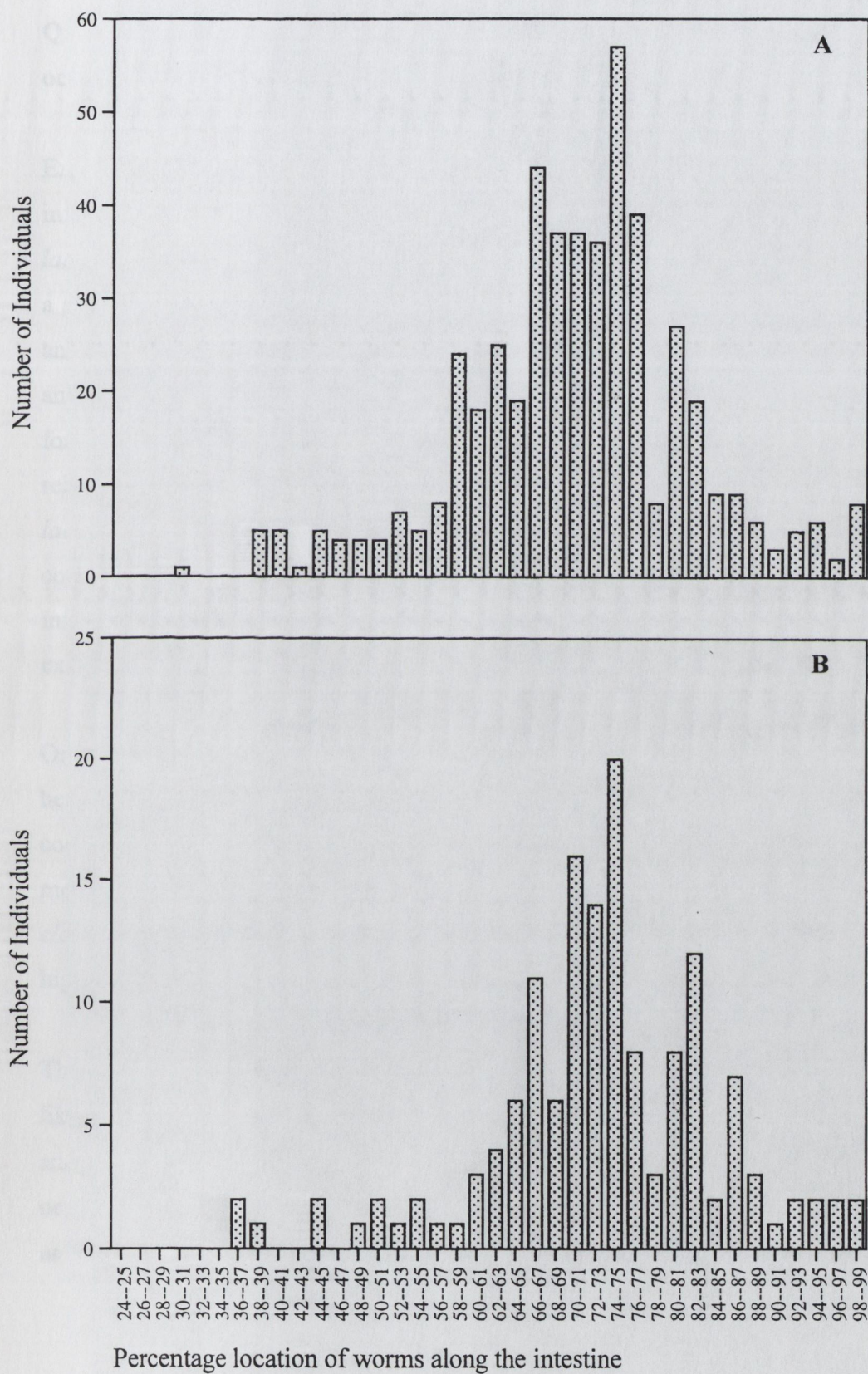


Fig 7.9 Niches for *P. laevis* when it occurred alone (A) and when it co-occurred with *A. clavula* (B) in Lough Feeagh, in November.

7.8 Discussion

Q. Is there a difference between the populations characteristics of *P. laevis* occurring alone and *P. laevis* co-occurring with *A. clavula*?

Examination of results revealed that for all months more *P. laevis* occurred in single infections. A total of 401 *P. laevis* co-occurred with *A. clavula* compared to 1319 *P. laevis* occurring alone. Kendall's tau non-parametric correlation co-efficient revealed a significant negative correlation between the abundance of *P. laevis* and *A. clavula* and two-way analysis of variance revealed significant differences between the lengths and weights of *P. laevis* in single and concurrent infections of *A. clavula*. Although, for both length and weight analyses, month was the most significant factor in the relationship. In nearly all cases mean length and weight values were higher for *P. laevis* co-occurring with *A. clavula*. When two-way analysis of variance was used to compare the lengths and weights of *P. laevis* in low, medium and high intensity infections occurring alone and co-occurring with *A. clavula*, a significant difference existed between weights, but no significant difference existed between lengths.

On the basis of these results it appeared that some type of interaction occurred between *P. laevis* and *A. clavula*. Results from the Kendall's tau correlation coefficient suggest that *P. laevis* had a negative effect on *A. clavula*. However, when mean length and weight values were examined it appeared that the presence of *A. clavula* had a beneficial effect on *P. laevis*, and when results for low, medium and high intensity infections were examined there was no obvious pattern.

The significant differences in the mean length and weight values reported were more likely to be a reflection of the differences in sample size between *P. laevis* in single and concurrent infections, rather than differences in actual length and weight values or as a result of a beneficial effect of *A. clavula*. In chapter six it was suggested that as the number of parasite individuals recorded in an individual fish increased, their

mean length and weight values decreased, it appears that the same situation occurred for *P. laevis* in single and concurrent infections.

Table 7.12 Sample number, prevalence, mean abundance and mean intensity values for *A. clavula* when it occurred in Clogher Lake, with *P. laevis* in Lough Feeagh and alone in Lough Feeagh†.

	Clogher Lake	L. Feeagh + <i>P. laevis</i>	L. Feeagh alone
Total Sample			
Number	161	379	143‡
% Prevalence	86.3	30.3	38
Mean Abundance (S.D.)	53.2(82.3)	3.1(10.7)	3.6(11.3)
Mean Intensity (S.D.)	90.1(93.2)	10.1(17.5)	11(17.7)
April			
Number	63	60	31
% Prevalence	93.7	15	12.9
Mean Abundance (S.D.)	58.2(77.5)	0.7(3.9)	0.8(3.3)
Mean Intensity (S.D.)	62.2(78.5)	4.3(5.1)	6.5(7.9)
May			
Number	39	111	37
% Prevalence	94.9	38.7	51.4
Mean Abundance (S.D.)	45.1(55.2)	3.9(12)	3.1(6.2)
Mean Intensity (S.D.)	47.5(55.6)	9.3(17.2)	8.4(2.9)
August			
Number	28	113	43
% Prevalence	42.9	29.8	30.23
Mean Abundance (S.D.)	6.6(13.7)	3.7(12.5)	5(15)
Mean Intensity (S.D.)	15.5(17.7)	12.3(20.5)	16.6(24)
November			
Number	31	95	32
% Prevalence	100	31.6	34.38
Mean Abundance (S.D.)	95.2(125.4)	2.8(9.7)	4.9(14.7)
Mean Intensity (S.D.)	95.2(125.4)	8.9(15.8)	14.4(22.7)

† = Values refer to wild and stocked fish in Lough Feeagh; ‡ = Refers to the number of fish examined from Lough Feeagh which did not have *P. laevis*.

The sample size, prevalence mean abundance and intensity values are presented for *A. clavula* when it occurred alone and when it occurred with *P. laevis* in Lough Feeagh. The same values are presented for *A. clavula* from Clogher Lake, as a comparison (Table 7.12). A similar situation occurred for *A. clavula* as occurred for *P. laevis*, in all cases, with the exception of May the mean abundance and mean intensity values were higher for *A. clavula* when it occurred alone. Similarly, in all cases except for April, the prevalence of *A. clavula* was higher when it occurred alone, however prevalence values for *A. clavula* in August and November were comparable between the two groups. This data supports the theory that *P. laevis* had some type of negative effect on *A. clavula*. When the values recorded for Lough Feeagh were compared to Clogher Lake, they were substantially lower in nearly all cases. August was the only month when mean abundance and mean intensity values recorded in Lough Feeagh were in any comparable to the values recorded for Clogher Lake (Table 7.12).

Kennedy and Moriarty (1987) examined the co-occurrence of *A. lucii* and *A. anguillae* in eels in Ireland. They showed that *A. lucii* was the dominant species and was over-dispersed throughout the eel population in all sample years, and it most frequently occurred as a single species infections, whereas, *A. anguillae* occurred most often in concurrent infections and its dispersion was close to random at most times. The proportion of the two species also remained constant over time. The situation described for *A. lucii* parallels the situation recorded for *P. laevis* in Lough Feeagh. Also *A. lucii* and *A. anguillae* did not appear to show any resource partitioning in space or time. However, they concluded that when one congener dominated to the extent that *A. lucii* did, whilst the other was as rare as *A. anguillae* was, interspecific competition must be considered as an explanation.

The situation in Lough Feeagh was similar to that described by Kennedy and Moriarty (1987), however there were a number of important differences. *P. laevis* and *A. clavula* are not congeneric species, thus were not as closely related as *A. lucii* and *A. anguillae*. Although *P. laevis* was the most dominant acanthocephalan species in Lough Feeagh overall, *A. clavula* was certainly not as subordinate as *A. anguillae* was

in Lough Derg. In all sample months with the exception of April, the prevalence values recorded for *A. clavula* when it occurred with *P. laevis* in Lough Feeagh, although lower, were comparable to the values recorded for *A. clavula* when it occurred alone (Table 7.12). Thus, it appeared that asymmetry, with one species dominating and the subordinate species occurring at low density, as a result of exploitation competition as predicted by Dobson (1985) and as demonstrated by Kennedy and Moriarty (1987) did not occur in Lough Feeagh.

In a later study Kennedy (1992) examined the interactions between *A. lucii* and *A. anguillae* in eels in more detail. He demonstrated that in single species infections each species had a distinct niche but could occupy much of the intestine even if it did not usually do so, and the fundamental niche of each species overlapped with that of the other. This situation was also found in Lough Feeagh, although *P. laevis* tends to occupy a more posterior location (Kennedy, 1985; This study, Tables 5.1-5.3) and *A. clavula* tends to occupy a more anterior position (Kennedy and Lord, 1982; This study, Tables 5.5-5.7). Kennedy (1992) also suggested that when both species were found in the same locality, conjoint occurrence, especially at equal intensities were uncommon in individual eels. He identified two different types of interactions, and the way in which species interacted depended on the absolute and relative densities of each species.

In the first situation where one species totally dominated the other, as demonstrated by Kennedy and Moriarty (1987), the interaction was asymmetrical. In the second situation where both species co-occurred in equal high density infections the interaction was symmetrical and the fecundity of neither species was affected. The situation recorded for *P. laevis* and *A. clavula* in Lough Feeagh was between the two scenarios, *P. laevis* did not totally dominate *A. clavula*, nor did both species co-occur in equal high intensity infections.

Bates and Kennedy (1990) examined the potential for interactions between *P. laevis* and *A. anguillae* in experimental rainbow trout. They showed that the presence of *P.*

laevis in the intestine reduced the range of the intestine occupied by, and the survivorship of, *A. anguillae*. They also showed that at high densities niche segregation occurred and niche overlap was reduced, and as a result individuals tended to be more aggregated in their distribution and were found in association with their conspecifics rather than their congeners. They considered this to be indicative of interspecific competition, which was non-reciprocal, as *P. laevis* remained unaffected by an increase in the number of *A. anguillae* present. A similar situation seemed to occur for *P. laevis* and *A. clavula* in Lough Feeagh. In all cases the niche width of *A. clavula* was smaller when it occurred in low, medium and high intensity infections of *P. laevis*, than when it occurred in low, medium and high intensity infections in the total sample. However, as suggested by Kennedy (1992), at lower intensities of each species competitive interactions would be less severe and so changes in distribution would be less apparent.

In contrast to the earlier study (Bates and Kennedy, 1990), Bates and Kennedy (1991b) could find no evidence of any interactions competitive or otherwise in mixed infections of *P. laevis* and *A. anguillae* in eels at low or high infection levels. However in the original experiments (Bates and Kennedy, 1990) rainbow trout were used. They cannot be considered as a natural native host for *P. laevis* and *A. anguillae* but rather a neutral host whereas in this study the eel was the preferred definitive host for *A. anguillae* but an unsuitable host for *P. laevis*.

In conclusion, it appears that in Lough Feeagh *A. clavula* had no effect on *P. laevis*, but it is likely that *P. laevis* had some negative effect on the population biology of *A. clavula*. The results from Lough Feeagh can only be tentatively compared to the studies mentioned above, as Bates and Kennedy (1990, 1991b) only examined *P. laevis* and *A. anguillae* in an experimental setting and Kennedy and Moriarty (1987) and Kennedy (1992) examined the interactions between the congeneric species *A. lucii* and *A. anguillae* in eels. No studies have yet examined the interactions between *A. clavula* and *P. laevis* in wild or stocked trout.

The behaviour of *P. laevis* in Lough Feeagh trout was probably quite analogous to the behaviour of *A. lucii* in eels, in that *P. laevis* was the numerically superior parasite, and its population biology characters were not affected by the presence of other species. Similarly, the behaviour of *A. clavula* in trout in Lough Feeagh was probably analogous to the behaviour of *A. anguillae* in the experimental infections described by Bates and Kennedy (1990), although it was not as subordinate as *A. anguillae*. Also, the differences in the mean length and weight values between *P. laevis* in single and concurrent infections were probably related to sample size, rather than any actual differences in length or weight. However the lack of published literature on the lengths and weights of *P. laevis* when it co-occurs with *A. clavula*, indeed the lack of literature on the co-occurrence of *A. clavula* and *P. laevis* in general meant it was not possible to directly compare the results of this study with those of any other.

Q. Is there a difference between the population characteristics of female *P. laevis* occurring alone and female *P. laevis* co-occurring with *A. clavula*?

There was a significant difference in the mean length of female *P. laevis* between single and concurrent infections but no significant difference in the mean weights of *P. laevis* in single and concurrent infections. In both cases month was the most significant factor in the two-way analysis performed. In nearly all cases the mean length and weight values were higher for *P. laevis* co-occurring with *A. clavula*. There was no significant difference in the mean length or weight values of stage I, II or III *P. laevis* between single and concurrent infections, but in all cases length and weight values were higher for *P. laevis* in concurrent infections.

Kennedy (1992) also reported no significant difference in the mean weights of *A. lucii* or *A. anguillae* of the same sex and maturity status between single and conjoint infections. He showed that the proportion of female parasites reaching full maturity varied between 69% and 93% in single species infections and between 64% and 85% in co-equal infections. However, he noted that when one species completely dominated the other, the proportion of females of the inferior species declined whilst

that of the dominant species remained unchanged. For *P. laevis* in Lough Feeagh, 22% of the female sample reached full maturity in single species infections and 13% of the total sample reached full maturity in concurrent infections. A similar drop occurred for female *P. laevis* of stage II maturity, whereas the proportion of female *P. laevis* of stage I maturity increased. This result would suggest that the presence of *A. clavula* tended to decrease the proportion of female *P. laevis* which attained full maturity in trout in Lough Feeagh (Table 7.9).

Bates and Kennedy (1990) demonstrated that *P. laevis* and *A. anguillae* differed in their rate of maturation. At 56 days post infection some *A. anguillae* had reached stage III maturity whereas *P. laevis* had only reached stage II maturity, however at 112 days post infection both species were producing mature acanthors. They also suggested that *P. laevis* in high-density infections, 56 days post infection, had a preferred site for maturation. However they could detect no pattern of maturation in relation to the numbers of each species.

In the previous section it was concluded that *A. clavula* had no effect on the population characters of *P. laevis*. The results from this section would suggest that the presence of *A. clavula* decreased the proportion of mature stage III *P. laevis* present, which according to Kennedy (1992) would suggest that *A. clavula* was the dominant parasite species. Also, in all cases *P. laevis* were longer and heavier in concurrent infections. However it is likely that the difference in the proportion of stage III female *P. laevis* and the higher mean length and weight values recorded for stage I, II and III *P. laevis* in concurrent infections was not related to the presence of *A. clavula* but to the absolute density of *P. laevis*. Thus, the fact that fewer *P. laevis* co-occurred with *A. clavula* meant that the potential for intraspecific competition between *P. laevis* worms was reduced, which explains the increased mean length and weight values recorded. It is likely that the reduction in the number of stage III *P. laevis* also results from the fact that fewer *P. laevis* co-occurred with *A. clavula*. When *P. laevis* occurred alone, 368 stage I, 96 stage II and 129 stage III females were recorded,

compared to 113 stage I, 17 stage II and 19 stage III females for *P. laevis* co-occurring with *A. clavula*.

Q. Is the niche of *P. laevis* when it occurs alone comparable to the niche of *P. laevis* when it occurs with *A. clavula*?

Two-way analysis of variance revealed no significant difference between the distribution of *P. laevis* in single and concurrent infections. Mean position values were slightly more posterior for *P. laevis* in concurrent infections in August and November, and for the total sample, however in all cases values were comparable to the values recorded for *P. laevis* occurring alone. Similarly niche width values for *P. laevis* in single and concurrent infections were comparable for all months and for the total sample. Finally, the deviations about the mean and the median values were also comparable between *P. laevis* in single and concurrent infections.

Kennedy and Moriarty (1987) examined the potential for interaction between *A. lucii* and *A. anguillae* in wild eels. They could find no evidence for the competitive displacement of *A. lucii* by *A. anguillae* or vice versa, or any evidence for resource partitioning in space. In a later paper Kennedy (1992) demonstrated that when *A. lucii* and *A. anguillae* co-occurred at equal and high densities the mean position remained unchanged but the variances of both species about the mean median position declined and niche overlap was reduced. In Lough Feeagh the variance values about the mean, the median values, and the niche width values were comparable between *P. laevis* in single and concurrent infections. Thus, indicating that the distribution of *P. laevis* was not reduced in the presence of *A. clavula*.

Bates and Kennedy (1991b) examined the potential for interaction between *P. laevis* and *A. anguillae* in their natural hosts, chub and eel. Chub proved to be unsuitable laboratory hosts for *P. laevis* and experiments using chub were discontinued. However in eels the authors could find no evidence of either species being lost from any particular region of the intestine, or of an exclusion zone. Thus they concluded

that there appeared to be no evidence of interspecific interactions positive or negative between *P. laevis* and *A. anguillae* in eels. In contrast Bates and Kennedy (1990) demonstrated in the laboratory that the presence of *P. laevis* in rainbow trout reduced the range of the intestine occupied and the survivorship of *A. anguillae* and that the interaction was non reciprocal, as the presence of *A. anguillae* did not affect *P. laevis*.

For brown trout in Lough Feeagh it can be concluded that the presence of *A. clavula* had no effect on the niche occupied by *P. laevis*. This result is in agreement with the findings of Kennedy and Moriarty (1987) and Kennedy (1992) who suggested that where one species dominated the other, i.e. an asymmetrical interaction, the results of interspecific competition would manifest themselves in the subordinate species. Although *P. laevis* did not dominate *A. clavula* in trout to the same extent that *A. lucii* dominated *A. anguillae* in eels, and thus it seemed that no marked asymmetry occurred, it would be interesting to see if *P. laevis* had any negative effect on the population biology characteristics of *A. clavula* in single and concurrent infections. Unfortunately it has not been possible to examine this scenario, although results from Table 7.12 indicate that such a situation could be occurring. Also, data on the niches occupied by *P. laevis* and *A. clavula* from previous sections of this thesis (Chapter 5, Tables 5.6-5.13) suggest that *P. laevis* had some effect on *A. clavula* and although the nature of the effect was unclear, it is highly likely that *P. laevis* inhibited *A. clavula* to some degree.

General Discussion

General Discussion

The present investigation set out to examine a number of hypotheses, the first of which was whether the parasite communities of trout from Clogher Lake and Lough Feeagh were characteristic of trout parasite communities in the west of Ireland and whether they were also characteristic of brown trout parasite communities in general. Clogher Lake was chosen as the 'control' lake in this study as it is in the same geographical area as Lough Feeagh and it contains a large stock of unmanaged wild brown trout. In the first instance, the component and infra communities of trout in Clogher Lake were compared to a previous study on trout from Lough Feeagh by Molloy *et al.* (1995a), and to a study on trout from Lough Owennamarve in Co. Donegal by Byrne *et al.* (2000).

On the basis of these comparisons a dichotomous classification for parasite communities in the west of Ireland was constructed. Clogher Lake and Lough Owennamarve represented parasite communities which were typical of mesotrophic systems, and Lough Feeagh represented a parasite community which was typical of oligotrophic systems. The parasite community of trout from Clogher Lake was then compared to parasite communities in brown trout from Scotland (Dorucu *et al.*, 1995) and Norway (Hartvigsen and Halvorsen, 1993). In this situation the parasite community recorded in Clogher Lake was comparable with, but richer than the parasite communities from Scotland and Norway. However, as demonstrated by Kennedy and Hartvigsen (2000), it was a suite of four trout specialists which occurred commonly that gave a degree of predictability to the community composition. Thus the parasite community recorded for brown trout in Clogher Lake could be considered as typical of that of brown trout in the west of Ireland and of brown trout in general.

The parasite community recorded for brown trout from Lough Feeagh in the present study was also compared to the parasite community recorded for trout in Lough Feeagh by Molloy *et al.* (1995a). Five parasite species were recorded in the present study, which were not recorded by Molloy *et al.* (1995a). When examined in detail it

appeared that of the five species, only the nematode *Rhabdochona* sp. could have been a new introduction to the lake. However it seems likely that this species either became locally extinct and a rescue effect from a nearby source permitted its recolonisation of the lake, or it was always present in the lake, but decreased to such a low level that was not recorded by Molloy *et al.* (1995a). Comparison of infra and component community results revealed that in terms of parasite composition both of these studies were similar, but in terms of structure they were considerably different. Thus, the parasite community recorded for trout from Lough Feeagh in the present study was essentially a richer version of the community recorded for trout in Lough Feeagh by Molloy *et al.* (1995a).

When the parasite communities of brown trout from Lough Feeagh from the present study were compared with those of Clogher Lake, a number of similarities appeared. At the component community level the same suite of trout specialists (Kennedy and Harvigsen, 2000) occurred in both lakes, providing a degree of predictability to the community. However stochastic and/or environmental processes (Esch *et al.*, 1988) also appeared to have an effect on the structure of the parasite community. Thus, the composition of the parasite component communities of brown trout from Clogher Lake and Lough Feeagh were comparable, although their structures differed. However it was concluded that the parasite community of brown trout from Lough Feeagh (in the present study) 'moved up the scale', therefore invalidating the dichotomous classification used for parasite communities of brown trout in the west of Ireland. The component community recorded for Lough Feeagh in this study was richer than that recorded for Lough Feeagh by Molloy *et al.* (1995a) but not as rich as that recorded for Clogher Lake or Lough Owennamarve. A similar pattern also occurred for the parasite infracommunities in Lough Feeagh and Clogher Lake.

The second hypothesis investigated in the present study was whether the parasite communities of wild and stocked trout were comparable at the component and infracommunity levels. When the parasite component communities of the total samples of wild and stocked trout in Lough Feeagh were compared, they were almost

identical in terms of community composition, but differed in terms of community structure. However, by just comparing the component communities for the total samples of wild and stocked trout the establishment and development of the parasite component community in stocked trout would have been overlooked.

Thus, when the parasite component communities were compared between wild and stocked trout on a monthly basis, a different pattern emerged. In May, almost all component community parameters were higher for wild trout, which was expected, as stocked trout had only been in Lough Feeagh for a few weeks. In August, the component community of stocked trout developed to the point where it was comparable to that of wild trout, and by November the component community recorded for stocked trout was richer than that recorded for wild trout. Therefore, although the end points for the parasite component communities of wild and stocked trout were almost identical, the 'process' of arriving at these endpoints differed.

A similar pattern occurred when the infracommunity parameters of wild and stocked trout were compared. For the total infracommunities of wild and stocked trout values were comparable, but only when infracommunity parameters were compared on a monthly basis was it possible to examine the process of establishment and development of the parasite community. Infracommunity parameters were higher for wild trout in May. In August the parasite infracommunity was richer for stocked trout but more diverse for wild trout, and in November all infracommunity parameters with the exception of the dominance indices were higher for stocked trout. Thus it appears that the parasite component and infracommunities in stocked trout developed from a 'naïve state' into mature parasite communities in a few months.

The third main hypothesis examined in this study concerned the microhabitat selectivity and population biology of *P. laevis*. In the first instance the microhabitat selectivity of *P. laevis* and *A. clavula* were examined in wild and stocked trout. *P. laevis* preferably occupied a posterior position along the intestine, although site fidelity was poor. However, the distribution of *P. laevis* recorded in this study was

considered to be typical of the distribution of *P. laevis* in trout in Ireland. The mean position of *P. laevis* in stocked trout was somewhat more anterior than that recorded in wild trout. Kennedy *et al.* (1976) concluded that the distribution of *P. laevis* in the alimentary canal of fish was primarily determined by the process of liberation, activation and establishment of the parasite. It was considered likely, that some more 'favourable' microhabitat conditions existed in stocked trout which improved the activation and establishment of *P. laevis*, thus resulting in a more anterior distribution in the intestine.

When the microhabitat selectivity of *A. clavula* was examined in detail, it was concluded that the same patterns of distribution occurred for *A. clavula* in Lough Feeagh and Clogher Lake. The parasite preferentially occupied the middle portion of the intestine, but similar to the situation with *P. laevis*, its site fidelity was poor. The same pattern of distribution occurred for *A. clavula* in wild and stocked trout. Examination of the distribution of *P. laevis* in low, medium and high intensity infections of *A. clavula* revealed that *A. clavula* appeared to have no effect on the distribution of *P. laevis*. Similarly *P. laevis* in low, medium and high intensity infections appeared to have no effect on the distribution of *A. clavula*.

In terms of population biology, the size recorded for *P. laevis* in the present study was generally comparable to the size recorded for *P. laevis* by Molloy *et al.* (1995b). Although, the mean parasite weight values recorded for *P. laevis* by Molloy *et al.* (1995b) were larger, it is likely that the greater number of worms examined outside the 'summer peak' in the present study affected the overall mean weight value recorded. Kennedy *et al.* (1978) proposed that *P. laevis* existed as three separate strains an English strain, an Irish strain and a marine strain. This sample of the Irish strain of *P. laevis* from brown trout appears to fit the description of a natural or preferred definitive host for *P. laevis* in terms of parasite size, however in terms of maturity status this sample appears to fall into the second host category, a suitable host, as defined by Hine and Kennedy (1974). This result is in agreement with the observations of Molloy *et al.* (1995b).

When the population biology of *P. laevis* was compared between wild and stocked trout a striking difference in the maturity status of female *P. laevis* in stocked trout was observed. The majority of female *P. laevis* in stocked trout worms were of stage I maturity and no mature female *P. laevis* were recorded. Although a number of potential reasons were put forward to explain this difference in the population biology of *P. laevis* between wild and stocked trout, such as the size of females in stocked trout, the lower number of male worms recorded and possible physiological factors associated with stocked trout. The exact reason for this difference in maturity status of female *P. laevis* between wild and stocked trout remains unclear.

The final hypothesis examined in this study concerned the potential for interaction between *P. laevis* and *A. clavula*. Examination of size and population biology data for *P. laevis* suggests that some 'type' of interaction occurred between *P. laevis* and *A. clavula*. When the total sample of *P. laevis* was examined it was concluded that *A. clavula* had no effect on *P. laevis*, however it was considered likely, although not possible to examine in this study, that *P. laevis* had some negative effect on *A. clavula*. A comparison between the prevalence and abundance values for *A. clavula* in Clogher Lake and Lough Feeagh also presents indirect evidence for the negative effect of *P. laevis* on *A. clavula*. In contrast, when the total sample of female *P. laevis* was examined it appeared that *A. clavula* had some type of negative effect, as fewer stage III female *P. laevis* occurred in the presence of *A. clavula*. However, it was considered likely that the reduction in the number of stage III *P. laevis* co-occurring with *A. clavula* was not as a result of any negative effects of *A. clavula*, but resulted from the fact that fewer *P. laevis* co-occurred with *A. clavula*. The fact that the distribution of *P. laevis* was not reduced in the presence of *A. clavula* supports this theory.

The present study provides evidence on the interaction of a number of parasite species pairs, *A. clavula* - *P. laevis*, *E. crassum* - *C. farionis* and *E. crassum* - *A. clavula*. More importantly this work along with other studies (Halvorsen and

MacDonald, 1972; Dorucu *et al.*, 1995; Lyndon and Kennedy, 2000) supports the growing body of evidence which suggests that the traditional view, that parasite communities in isolationist species poor systems are non-interactive is wrong. Current work, including the present study, suggests that the parasite communities in species poor isolationist systems not only have the potential to interact, but actually do so with greater frequency and between greater numbers of species that was ever previously predicted.

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Appendix
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Appendices

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Appendix 1: Table 1
 Significant least squares difference post hoc test results for *A. clavula*

Sample Months	Difference	Std. Error	Prob
May 97 - April 97	3.43	0.64	0.0001
August 97 - May 97	-4.03	1.19	0.0007
November 97 - August 97	-3.66	1.14	0.0012
April 98 - April 97	1.46	0.55	0.0103
April 98 - May 97	-2.02	0.52	0.0001
May 98 - April 97	-1.9	0.73	0.0092
May 98 - November 97	2.36	0.61	0.0001
May 98 - April 98	-3.31	0.63	0.0001
August 98 - November 97	8.38	3.86	0.0297
February 99 - May 97	-2.72	0.69	0.0001
February 99 - May 98	2.61	0.78	0.0007

Appendix 1: Table 2
 Significant least squares difference post hoc test results for *C. farionis*

Sample Months	Difference	Std. Error	Prob
August 97 - April 97	4.59	1.12	0.0001
August 97 - May 97	5.32	1.92	0.0056
November 97 - April 97	4.63	0.95	0.0001
November 97 - May 97	5.36	1.82	0.0032
April 98 - August 97	-4.81	1.01	0.0001
April 98 - November 97	-4.85	0.81	0.0001
May 98 - April 97	3.83	0.87	0.0001
May 98 - May 97	4.56	1.78	0.0105
May 98 - April 98	4.06	0.72	0.0001
August 98 - April 97	7.77	2.06	0.0001
August 98 - May 97	8.50	2.58	0.0010
August 98 - April 98	7.99	2	0.0001
February 99 - April 97	7.10	1.18	0.0001
February 99 - May 97	7.83	1.95	0.0001
February 99 - November 9	2.47	1.24	0.0457
February 99 - April 98	7.732	1.07	0.0001
February 99 - May 98	3.27	1.18	0.0056

Appendix 1: Table 3
Significant least squares difference post hoc test results for *E. crassum*.

Sample Months	Difference	Std. Error	Prob
August 97 - April 97	-4.35	1.97	0.0270
April 98 - August 97	4.39	1.91	0.0221
May 98 - May 97	4.91	2.39	0.0406
May 98 - August 97	4.79	1.96	0.0149
February 99 - April 97	12.96	2.12	0.0001
February 99 - May 97	17.43	2.81	0.0001
February 99 - August 97	17.31	2.46	0.0001
February 99 - November 97	15.15	2.22	0.0001
February 99 - April 98	12.92	2.07	0.0001
February 99 - May 98	12.52	2.11	0.0001
February 99 - August 98	14.49	2.36	0.0001

Appendix 2: Table 1
 Significant least squares difference post hoc test results for *P. laevis* in wild trout

Sample Months	Difference	Std. Error	Prob
May 98 - April 97	-4.66	1.39	0.0008
May 98 - May 97	-3.12	0.98	0.001
August 97 - April 97	-7.66	1.41	0.0001
August 97 - May 97	-6.12	0.99	0.0001
August 97 - May 98	-2.99	1.03	0.003
August 98 - April 97	-5.51	1.65	0.0008
August 98 - May 97	-3.96	1.31	0.002
November 97 - April 97	-11.96	1.99	0.0001
November 97 - May 97	-10.43	1.73	0.0001
November 97 - May 98	-7.3	1.74	0.0001
November 97 - August 97	-4.31	1.75	0.014
November 97 - August 98	-6.46	1.95	0.0009
November 98 - April 97	-8.25	1.62	0.0001
November 98 - May 97	-6.71	1.27	0.0001
November 98 - May 98	-3.58	1.3	0.006

Appendix 2: Table 2
 Significant least squares difference post hoc test results for *P. laevis* in stocked trout

Sample Months	Difference	Std. Error	Prob
August 97 - May 97	12.99	5.94	0.029
August 98 - Novemer 97	16.3	5.36	0.002
August 98 - May 98	16.86	5.62	0.003
November 98 - August 97	-15.72	5.42	0.004

Appendix 2: Table 3
 Significant least squares difference post hoc test results for *A. clavula* in wild trout

Sample Months	Difference	Std. Error	Prob
May 98 - April 97	-9.19	2.21	0.0001
August 97 - April 97	-24.14	2.33	0.0001
August 97 - May 97	-17.97	4.76	0.0001
August 97 - May 98	-14.94	1.48	0.0001
August 98 - April 97	-19.5	2.8	0.0001
August 98 - May 97	-13.36	5.02	0.007
August 98 - May 98	-10.32	2.15	0.0001
August 98 - August 97	4.62	2.27	0.04
November 97 - April 97	-19.03	9.08	0.03
November 98 - April 97	-29.68	2.38	0.0001
November 98 - May 97	-23.52	4.76	0.0001
November 98 - May 98	-20.48	1.57	0.0001
November 97 - August 97	-5.54	1.74	0.0014
November 98 - August 98	-10.16	2.32	0.0001

Appendix 2: Table 4
 Significant least squares difference post hoc test results for *A. clavula* in stocked trout

Sample Months	Difference	Std. Error	Prob
August 97 - May 97	-14.74	2.88	0.0001
November 97 - August 97	20.14	2.78	0.0001
May 98 - August 97	13.81	1.95	0.0001
May 98 - November 97	-6.34	2.81	0.025
August 98 - August 97	10.84	2.15	0.0001
August 98 - November 97	-9.31	2.95	0.002
November 98 - August 97	10.37	2.08	0.0001
November 98 - November 9	-9.78	2.89	0.0008