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Prey consumption rates and growth of piscivorous brown trout in a subarctic watercourse

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ABSTRACT

Prey consumption rates of piscivorous brown trout, *Salmo trutta*, were studied in the Pasvik watercourse, which forms the border between Norway and Russia. Estimates of food consumption in the field were similar to or slightly less than maximum values from a bioenergetic model. The piscivore diet consisted mainly of vendace, *Coregonus albula*, with a smaller number of whitefish, *C. lavaretus*. Individual brown trout had an estimated mean daily intake of approximately 1·5 vendace and 0·4 whitefish, and a rapid annual growth increment of 7-8 cm year^{-1}. The total population of brown trout >25 cm was estimated as 8445 individuals (0·6 individuals ha^{-1}), giving an annual consumption of 1553880 (±405360 S.E.) vendace and 439140 (±287130 S.E.) whitefish for the whole watercourse. The rapid growth in summer of brown trout >25 cm indicated a high prey consumption rate.

Key words: *Coregonus* spp.; feeding; piscivory; *Salmo trutta*; vendace; whitefish.

INTRODUCTION

Predator-prey interactions may have an important role in regulating the population abundance and community structure of freshwater fish (Mittelbach & Persson, 1998). Establishing quantitative and reliable estimates of prey consumption rates in fish populations is an appealing approach for analysis of ecological interactions and a useful tool in fisheries management (Stewart *et al*., 1983; Gerking, 1994; Olson & Galvan-Magana, 2002; Pauly *et al*., 2002). In many freshwater systems, the brown trout *Salmo trutta* L. is an important piscivorous species, switching from invertebrates to fish predation at a size of about 20-25 cm (Campbell, 1979; L'Abée-Lund, 1992; Kahilainen & Lehtonen, 2002, 2003). When brown trout are feeding on fish, the prey consumption rates differ from those feeding on invertebrates, mainly because of higher energy intake and growth as a result of piscivorous behaviour and foraging (Garman & Nielsen, 1982; Elliott & Hurley, 2000).

For piscivorous brown trout, prey consumption rates may be calculated directly by using food consumption models based on gastric evacuation rates (Elliott, 1991; He & Wurtsbaugh, 1993), or indirectly from bioenergetics models (Forseth & Jonsson, 1994; Vehanen *et al.*, 1998; Elliott & Hurley, 2000) or radioisotope models (Forseth *et al*., 1992). However, the methods are based on different parameters with respect to important variables such as food availability, metabolic cost and temperature, which potentially may result in contrasting outcomes with respect to the estimates of consumption rate. Thus, comparing estimates from direct and indirect methods can provide valuable independent validation of field- and laboratory-measured parameters (Rice & Cochran, 1984; Héroux & Magnan, 1996), as well as testing the reliability of the different consumption estimates.

Studies that compare estimates of direct and indirect methods for prey consumption rates of piscivorous brown trout have not previously been published. The objectives of the present study were: (i) to estimate prey consumption rates of brown trout on a daily and seasonal basis, (ii) to compare these estimates with maximum prey consumption values obtained from a bioenergetic model, and iii) to estimate the growth of the piscivorous brown trout in the watercourse.

MATERIAL AND METHODS

STUDY AREA

The subarctic Pasvik watercourse originates from Lake Inari (1102 km^2) in northern Finland, runs north into Russia and then defines the border between Norway and Russia for a length of approximately 120 km. The Norwegian-Russian part of the watercourse has a total area of 142 km^2, a catchment area of 18404 km^2, and a mean annual water flow of 175 m^3 s^{-1}. There are altogether seven water impoundments (hydroelectric reservoirs) along the watercourse. Most rapids and waterfalls have disappeared, and today lakes and reservoirs linked together by short and slowly flowing river sections dominate the system. The mean annual amplitude in the water fluctuations is relatively small, usually less than 80 cm. The ice-free season in the lakes and reservoirs lasts from May/June to October/November. Mean water temperature during summer time is around 12º C with a maximum approaching 17-18º C. The lakes and reservoirs are oligotrophic with some humic impacts, neutral pH (6·11-7·07), and a Secchi-depth ranging from 2-6 m. Altogether 15 fish species have been recorded in the Pasvik watercourse. The most commonly occurring species in the lakes are whitefish *Coregonus lavaretus* (L.) *sensu lato*, vendace *C. albula* (L.), perch *Perca fluviatilis* L., pike *Esox lucius* L., burbot *Lota lota* (L.) and brown trout.

As there was a reduction in the recruitment potential of brown trout after the water regulation, a compulsory annual stocking of about 5000 large (total length >25 cm) brown trout was initiated in the watercourse. The whitefish occur as two different morphs; the sparsely gill-rakered whitefish (mean gill number 23·1, hereafter denoted s.r. whitefish), and the densely rakered form (mean number 33·0, hereafter denoted d.r. whitefish) (Amundsen *et al.*, 1999). The two whitefish morphs are easily separated and identified from differences in gill morphology (Amundsen *et al.*, 2004). Vendace is a non-native species that invaded the watercourse in the late 1980's, and has become a dominant species in the pelagic zone of the lakes and reservoirs (Amundsen *et al.*, 1999; Bøhn & Amundsen, 2001). Vendace and whitefish can be easily separated by the position of the mouth and the morphology of the gill rakers.

FISH SAMPLING

Brown trout sampling was carried out from June to October 1999 by local fishermen (13 person in total), using gill nets (primary 39-52 mm bar mesh size) and different sorts of fishing rod equipment. The gillnets were emptied once per day. A total of 393 fish were caught and measured by total length (range 23-68 cm, mean 36·6 cm) and mass (range 190-5000 g, mean 688 g). The stomach contents were removed and immediately deep-frozen for further analysis, and otoliths from wild brown trout were taken for age determination. Wild and stocked brown trout were distinguished by defining individuals with characteristic fin damage as stocked fish (Lund *et al.*, 1989), apart from 32 fish that were not classified by the fishermen. Therefore, 361 fish were used for the population estimates. Vendace and d.r. whitefish were sampled during June, August and September 1999, using pelagic gill nets with bar mesh sizes (knot to knot) of 8, 10, 12·5, 15, 18·5, 22, 26 and 35 mm. All fish (vendace, n=166 and d.r. whitefish, n=129) were measured in mm (fork length) and weighed in grams.

STOMACH CONTENT AND GROWTH ANALYSES

Brown trout stomach samples were analysed in the laboratory and the contents categorized into six main prey groups. Partially-digested fish prey items were identified to species by the remaining external features, and whitefish to morph by gill-raker examination. Other prey items, mainly aquatic insects (including Ephemeroptera, Trichoptera, Plecoptera, Odonata, Chironomidae and Coleoptera), were pooled into one group called invertebrates. The stomach contents of each individual fish were dried (65º C for >72 hours) and then weighed, keeping the different prey categories separate.

To determine growth of stocked brown trout, fish sampled were pooled over two-week intervals, providing a total of eight mean values (±95% CL) of total length and mass over the sampling season. To determine growth of wild brown trout, fish were aged using otoliths, and then mean values (±95% CL) of total length and mass were determine for each age group.

FOOD CONSUMPTION ESTIMATES

a) The food consumption model

The daily food consumption (C_{24}) was estimated using the modified Bajkov method (Bajkov, 1935; Eggers, 1977, 1979; Elliott & Persson, 1978):

$$C_{24} = 24\,SR \qquad (1)$$

where S is the mean mass of stomach contents and R is the instantaneous gastric evacuation rate. The mass of the stomach contents was expressed as g dry mass (DM) of prey per predator and standardized to that for a 700 g brown trout (g DM prey predator^{-1}), using a logarithmic regression (both axes on log scales) between stomach contents mass and fish mass. The standardization was validated by the absence of a significant correlation between the standardized stomach contents mass and fish size (P >0·05). Previously presented gastric evacuation rates of brown trout were used in the present study (Elliott, 1972, 1991). For piscivorous brown trout, the evacuation rate was calculated by the equation (Elliott, 1991):

$$R = 0{\cdot}0362\ e^{0{\cdot}114T} \qquad (2)$$

and for brown trout feeding on invertebrates by (Elliott, 1972):

$$R = 0{\cdot}053\ e^{0{\cdot}112T} \qquad (3)$$

where T was the water temperature (º C) . The fish samples were pooled over two-week intervals, providing a total of eight time periods over the sampling season. The water temperature was monitored continuously, and the mean water temperature for each period was used for the estimates of evacuation and consumption rates (Fig. 1c).

b) The bioenergetic model

The maximum food consumption of the Pasvik brown trout was estimated from the bioenergetic model developed for piscivorous brown trout by Elliott & Hurley (2000). The maximum daily energy intake (C_{IN}, cal day^{-1}) was given by:

$$C_{IN} = C_{max}\{(T\text{-}T_L)/(T_M\text{-}T_L)^b W^d\} \qquad (4)$$

where W was the wet mass of the brown trout (standardized to 700 g in the present study), d was the weight exponent (= 0·766), T was the water temperature (º C), C_{max} was the daily energy intake of a 1-g fish at the temperature T_M (= 18º C) for maximum energy intake (= 403·62 cal), T_L was the theoretical temperature at which energy intake was zero (= - 7·48º C), and b had the value of 3·002 (Elliott & Hurley, 2000). The theoretical value of T_L was well below the actual value for zero energy intake (c. 0º C) because there was a change in slope in the model at 6·8º C so that the decreasing daily energy intake did not attain zero until a theoretical temperature of - 7·48º C was reached (see Elliott & Hurley, 1998) The estimates of daily energy intake were converted and expressed in terms of dry mass using an energy value of 5·5 cal per mg dry mass (Winberg, 1971).

PREY SIZE

The length of undigested fish prey in the brown trout stomachs was measured to the nearest mm. For the two dominant prey categories, vendace and whitefish, wet and dry mass (65º C for >72 hours) were determined for a gill-netted sub-sample of 30 fish from each species, and the mass-length relationships were estimated by logarithmic linear regression (Table I). These relationships were then used to estimate the mean dry mass of the brown trout fish prey in order to calculate the number of fish prey consumed from the estimated food consumption rates.

BROWN TROUT POPULATION DENSITY

All stocked brown trout released in 1999 (n=5341, mean size 28·4 cm, mean mass 303 g) were marked by removal of the adipose fin. In the catches of brown trout from 1999, the marked fish were recorded in order to estimate the total population size (*N*), of brown trout with a length >25 cm, by using the Chapman modification of the Petersen method (Ricker, 1975):

$$N = (M+1)(C+1) / (R+1) \qquad (5)$$

where *M* is the total number of marked fish, *C* is the total capture of fish and *R* the recapture of marked fish. Computation of confidence limits (95% CL) was based on the assumption that recapture was successive and independent of time period, e.g. Poisson distributed (Ricker, 1975).

RESULTS

DAILY AND SEASONAL FOOD CONSUMPTION RATES

In total, vendace contributed 63% to the food intake of brown trout during the ice-free season, while d.r. whitefish made up 18% and s.r. whitefish 6% (Fig. 1). The importance of other fish prey such as burbot and nine-spined sticklebacks was low throughout the sampling period (in total <5%). Despite a low total amount of invertebrates eaten by brown trout during the season (11%), invertebrates represented the principal prey category in the first July sample (42%). However, the number of brown trout in this sample was only eight.

The estimates from the food consumption model showed an increase in the brown trout daily ration from approximately 0·9 g DM prey predator^{-1} in June to a peak of 5·8 g in late August and then decreased to 1·4 g in October (Fig. 1). The predicted values of the maximum daily food ration derived from the bioenergetic model exceeded the values estimated from the food consumption model, except for late August (Fig. 1). However, the discrepancy between estimates from the two models was not large for most samples with the estimates from the bioenergetics model usually lying close to or within the standard error (S.E.) of the estimates from the food consumption model. The most marked discrepancy was in the last period of July where the bioenergetic model gave 9·6 g vs 3·6 g DM prey predator^{-1} from the food consumption model. However, this was the smallest sample with only seven brown trout and therefore the field value may be an underestimate. Over the total season, the mean daily ration estimated from the food consumption and bioenergetic models was 3·3 ±1·4 S.E. g and 5·1 g DM prey predator^{-1}, respectively. The total piscivore consumption during the ice-free season was, according to the estimates from the food consumption model, equivalent to 1·55 kg prey fish (1·74 kg including invertebrates) for a brown trout of mean size, compared to 2·70 kg from the estimates of the bioenergetic model.

NUMBER OF VENDACE AND D.R. WHITEFISH CONSUMED

According to the estimates from the food consumption model, a single brown trout consumed approximately 1·5 (±0·4 S.E.) vendace and 0·4 (±0·2 S.E.) d.r. whitefish per day or a total of 184 (±48 S.E.) vendace and 52 (±34 S.E.) d.r. whitefish during the period from 15 June to 15 October (Table II). The mean individual consumption of vendace was relatively low in June and July (0·6 vendace pr day) with a significant peak in the second period of August (approx. 3·5 vendace pr day). In contrast, the brown trout ration never exceeded a ration of 1·0 d.r. whitefish pr day, independent of time period.

A total of 228 fin-tagged brown trout were recaptured in 1999 and the Chapman modified Petersen method estimated a total of 8445 (95% CL 7467-9267) brown trout >25 cm for the whole Pasvik watercourse in 1999 (0·6 individuals ha^{-1}). This results in a total prey consumption of 1553880 (±405360 S.E.) vendace and 439140 (±287130 S.E.) whitefish and represents an annual consumption of vendace and d.r. whitefish of 140 (±49 S.E.) fish ha^{-1} or 0·84 (±0·29 S.E.) kg ha^{-1} by the piscivorous Pasvik brown trout (Table II).

GROWTH

Brown trout stocked in June rapidly increased their mean length and mass during the summer season, with a mean length and mass increase of 7·4 cm and 380 g, respectively, when recaptured in October (Fig. 2a). Similarly, the mean length at age of wild brown trout increased at 7-8 cm/year, from 23 cm for 3-year old fish to 55 cm for 7-year old fish (Fig. 2b).

DISCUSSION

Vendace and d.r. whitefish were the dominant prey species in the brown trout diet, with a peak consumption level in August according to the estimates from the prey consumption model. In general, the daily energy intake of fish responds positively to temperature up to a given optimum and then decreases (Brett, 1971; Elliott, 1976). For piscivorous brown trout, the optimum temperature for growth was found to be 16-17º C in laboratory studies (Elliott & Hurley, 2000). At the maximum prey consumption rates in August the temperature varied between 12·4-14·8º C, which is close to the optimum temperature for growth when brown trout are feeding on invertebrates (Elliott, 1994). The observed maximum rates at lower temperatures might be explained by the study of Forseth & Jonsson (1994), who hypothesised that the optimum temperature for energy intake and growth among brown trout populations may be the result of natural selection and should be high in warmer localities and lower in cold environments. Brown trout predator feeding behaviour and prey consumption rates are also related to species composition, density, size-structure, habitat choice and behaviour of the prey (Popova, 1978; Wootton, 1998), and the coregonids in the watercourse (Amundsen *et al.*, 1999) are also found elsewhere to be a suitable prey species for brown trout (Vehanen *et al.*, 1998; Kahilainen & Lehtonen, 2002, 2003).

The two methods gave comparable estimates of the prey consumption rate, except for one small sample in late July. The bioenergetic model provides estimates of maximum food consumption rates, based on the conditional assumption that the brown trout are feeding to satiation. Hence, the estimates derived from the food consumption model indicate that brown trout in the Pasvik watercourse were feeding quite close to maximum ration. Despite few studies on comparable prey consumption rates for piscivorous brown trout, the mean daily ration in the present study corresponded well with estimates in another study that used a different bioenergetic method (Vehanen *et al*., 1998). In the latter study, high daily rations resulted in growth rates of 7-10 cm per year, comparable to the results of the present study.

For the stocked brown trout in the watercourse, a high proportion of small-sized fish prey, especially vendace, seems favourable for their ability to start feeding on fish and apparently enhance their daily ration. A similar piscivorous diet was found between wild and stocked Pasvik brown trout by Jensen *et al.* (2004), and indicated that stocked brown trout quickly adopt the feeding behaviour and habitat use of wild fish. The rapid growth in summer of brown trout > 25 cm also indicated a high prey consumption rate. Vehanen & Aspi (1996) investigated brown trout stocking in 33 Finnish lakes, and found a positive relationship between recapture of brown trout in systems where vendace were abundant. The recently invading vendace in the Pasvik watercourse may thus have a positive influence on the density of the brown trout population. On the other hand, an increase in the population size of brown trout may have regulatory effects on the vendace population. From the estimated daily ration of approximately 1·9 fish prey per brown trout, the total seasonal consumption of the brown trout population in the Pasvik watercourse compromised nearly 2 million prey fish. Our estimate of 1·55 prey fish per brown trout for the whole sampling period was close to that found by Vehanen *et al*. (1998), who estimated a mean consumption rate of 1·8 kg prey fish/year for a single brown trout. Vendace populations are frequently found to undergo cyclic oscillations, but this is usually related to high predation impacts on the zooplankton community and strong intraspecific competition (Hamrin & Persson, 1986; Sandlund *et al.*, 1991), and not to piscivorous predation. The estimated annual brown trout consumption of 140 fish ha^{-1} represents less than 10 percent of the pelagic coregonid density observed in the Pasvik watercourse in 2000 (Gjelland 2003). Thus, given the relatively low population abundance of 0·6 brown trout ha^{-1} in the watercourse, the overall predator effect on the vendace population may play a minor role, but this cannot be evaluated without more detailed information on the prey population density.

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TABLES

TABLE I. The relationship between length (*L*; cm) and wet mass (*WM*; g) and dry mass (*DM*; g) for vendace and whitefish in the Pasvik watercourse (p <0·001 for all regression).

Species	Range (cm)	Regression (ln W = ln a - b ln L)	r^2-value
Vendace	7·2 – 14·2	ln WM = 4·599 - 2·981 ln L	0·960
		ln DM = 6·609 - 3·238 ln L	0·974
Whitefish	6·8 – 15·3	ln WM = 4·842 - 3·121 ln L	0·987
		ln DM = 6·476 - 3·196 ln L	0·981

TABLE II. Estimated prey consumption (vendace and d.r. whitefish) of brown trout (length >25 cm) for the total sampling period from 15 June to 15 October (± S.E. for each estimated value).

	Individual consumption		Total population consumption		
Prey fish	(no. of prey)	(kg)	(no. ha^{-1})	(kg ha^{-1})	(no. of prey)
Vendace	184 ±48	1·10 ±0·28	109 ±29	0·65 ±0·17	1553880 ±405360
D.r. whitefish	52 ±34	0·32 ±0·21	31 ±20	0·19 ±0·12	439140 ±287130
Sum	236 ±82	1·42 ±0·49	140 ±49	0·84 ±0·29	1993020 ±692490

FIGURE LEGENDS

FIG. 1. Daily food consumption of brown trout (g DM prey predator^{-1}) with mean values for a standardized 700 g brown trout, (a) comparison of mean values from the food consumption model (solid line with S.E. as vertical lines) and maximum values from the bioenergetic model (▼), (b) diet composition based on the food consumption model, and (c) mean water temperature (T°C) in the Pasvik watercourse over two week intervals (with S.D. as vertical lines) from 15 June to 15 October. The number of fish measured is given at the top of the figure for each value.

FIG. 2. Temporal changes in mean length and mass of brown trout, (a) stocked fish during their first summer season after release, and (b) wild fish with increasing age. Vertical lines indicate 95% CL. The number of fish measured is given at the top of the figure for each value.

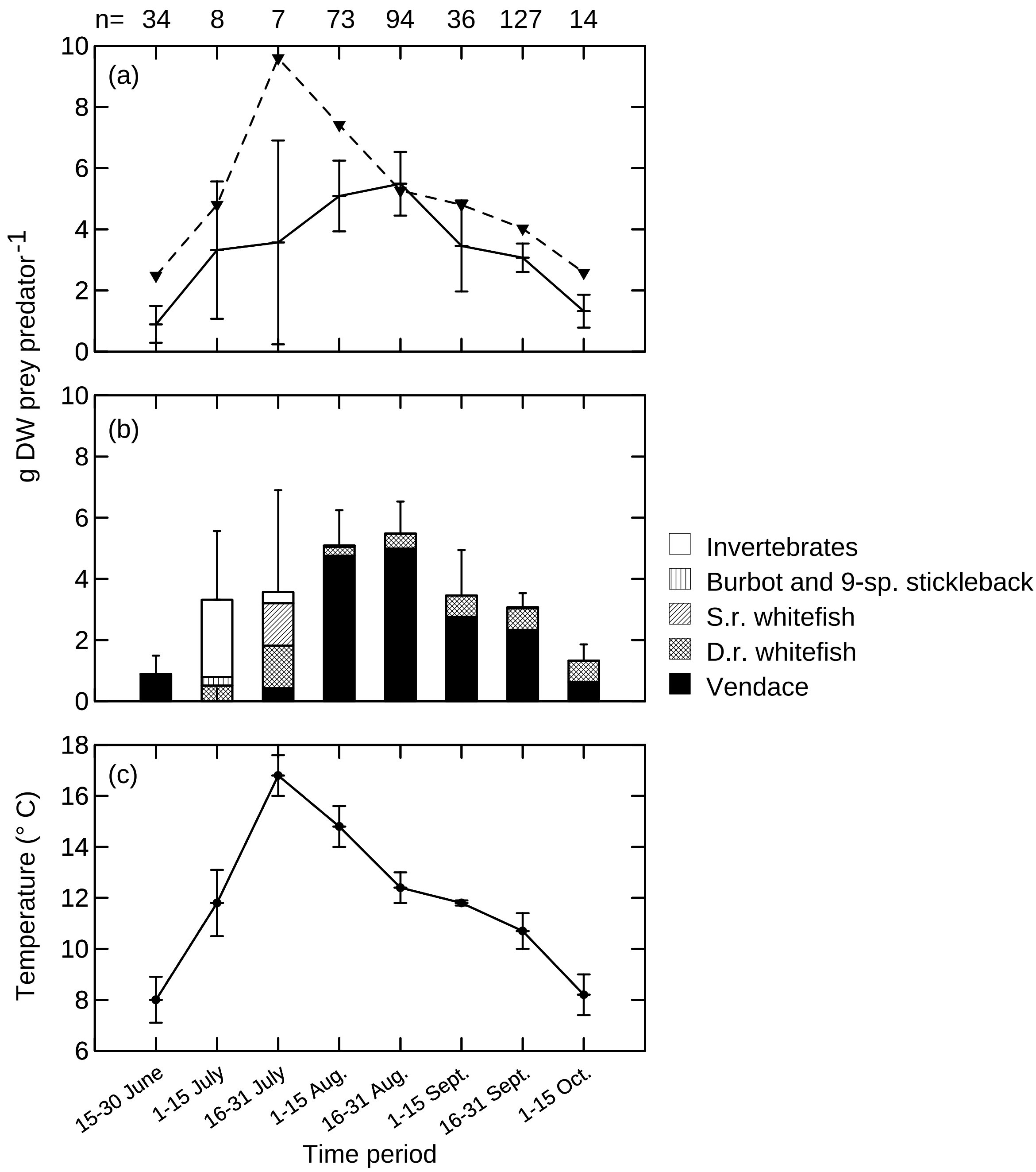
n= 34 8 7 73 94 36 127 14
(a)
(b)
(c)
g DW prey predator-1
Temperature (° C)
Invertebrates
Burbot and 9-sp. stickleback
S.r. whitefish
D.r. whitefish
Vendace
15-30 June
1-15 July
16-31 July
1-15 Aug.
16-31 Aug.
1-15 Sept.
16-31 Sept.
1-15 Oct.
Time period

FIG. 1.

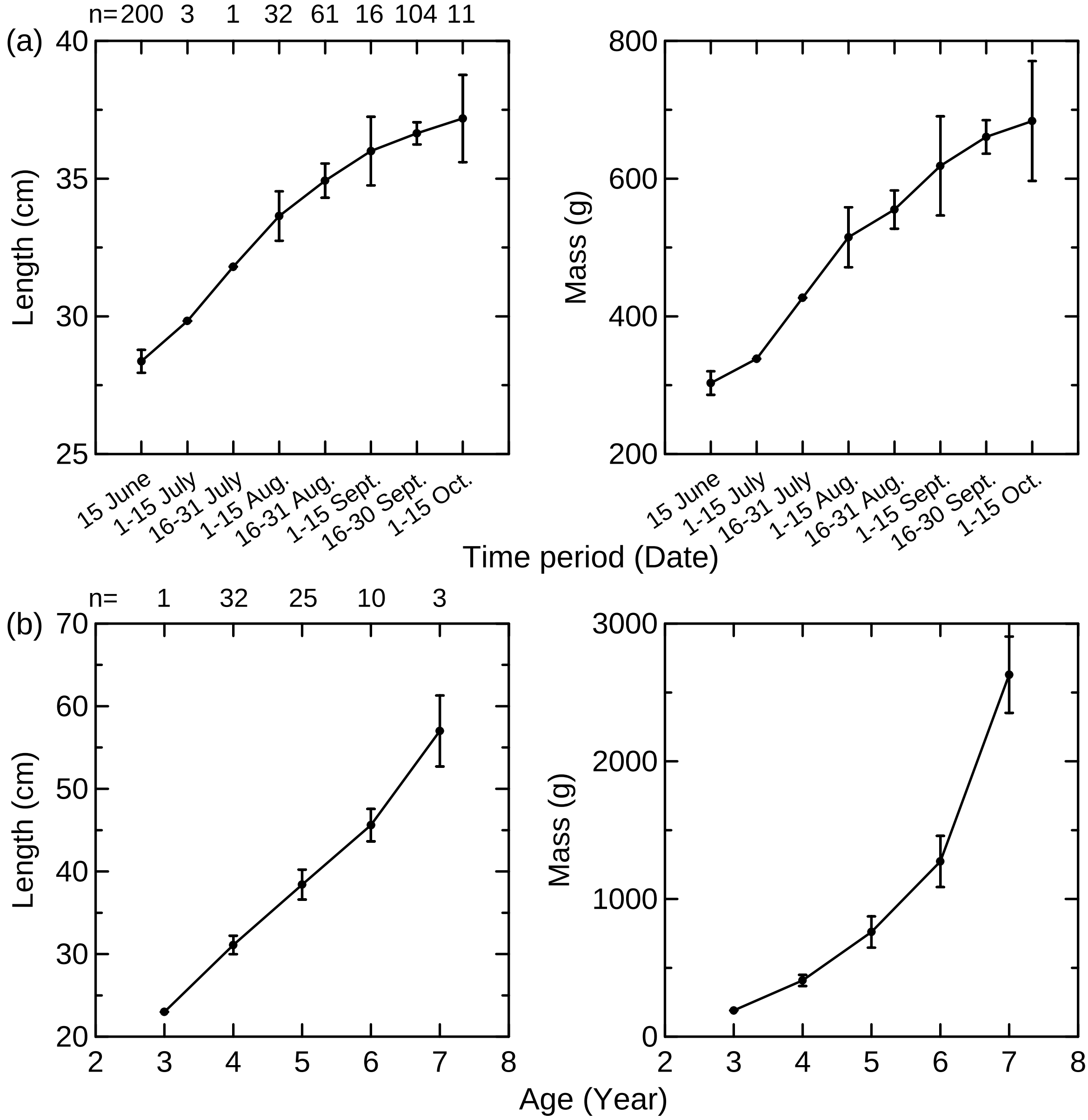
(a)
n=200 3 1 32 61 16 104 11
Length (cm)
Mass (g)
15 June
1-15 July
16-31 July
1-15 Aug.
16-31 Aug.
1-15 Sept.
16-30 Sept.
1-15 Oct.
Time period (Date)
(b)
n= 1 32 25 10 3
Length (cm)
Mass (g)
Age (Year)

FIG. 2.

*** Response to referees**

Dear Dr. Craig,

I enclose a revised version of MS 05-179. We have responded positively to all of the referee's comments, and have changed the text accordingly. We have added the number of brown trout measured to figure 2. These comments were most useful and are appreciated.

We feel that all these changes have produced a better paper and we hope that it is now acceptable.

Yours sincerely,

Hallvard Jensen