Behavioural strategy of large perch *Perca fluviatilis* varies between a mesotrophic and a hypereutrophic lake

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Behaviour of large perch *Perca fluviatilis* was studied in two lakes differing in environmental state *i.e.* mesotrophic *v.* hypereutrophic. A total of 20 adult perch *P. fluviatilis* (29–42 cm total length) in each lake were tagged with radio-transmitters, tracked and located eight times a day during six 24 h tracking periods over a year, enabling detection of differences in diel activity patterns and habitat use during summer and winter under two different environmental regimes. During summer, *P. fluviatilis* in the mesotrophic lake showed a distinct crepuscular activity pattern and a change from pelagic residency during daytime towards the littoral zone at night. In contrast, *P. fluviatilis* in the hypereutrophic lake were active during the entire diel cycle and were spread throughout the lake also during dark. During winter, crepuscular patterns of activity were seen in both lakes. Condition factor of large *P. fluviatilis* did not differ between the two lakes. Thus, it is suggested that *P. fluviatilis* in the hypereutrophic turbid lake adopted an alternative behaviour for successful foraging, being uniformly active throughout the diel cycle.

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Key words: activity; habitat use; lakes; radio-telemetry; turbidity.

INTRODUCTION

Predation is an important structuring mechanism in lake ecosystems where predators control the density of their prey with subsequent cascading effect on lower trophic levels (Carpenter & Kitchell, 1993; Fryxell & Lundberg, 1998). Predator–prey interactions may be controlled by several conditions that often change along a nutrient gradient, for instance habitat structure (Miner & Stein, 1996; Jacobsen & Berg, 1998; Carter *et al.*, 2010), water visibility (Utne-Palm 2002; Turesson & Brönmark, 2007; Ranåker *et al.*, 2012) and population structure and density of both prey fishes and piscivores (Jeppesen *et al.*, 2000). Predation success in hypereutrophic low-visibility waters is affected not only by constraints in vision but also by prey-encounter probability (Utne-Palm 2002; Turesson & Brönmark, 2007). The chance of encountering a prey varies in time and space and is affected by the density of prey as well as by behavioural patterns of both predator and prey fishes such as activity levels or habitat use. These encounter-rate variables may change along a nutrient gradient. For example, anti-predator behaviour of prey fishes such as schooling (which decrease

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encounters with predators) may be impaired in turbid water (Abrahams & Kattenfeld, 1997; Snickars *et al.*, 2004). In hypereutrophic lakes, the density of smaller prey fishes is likely to be high (Jeppesen *et al.*, 2000) compared with less nutrient-rich lakes. In combination, these interactions suggest that although reduced visibility in nutrient-rich lakes may impair the predators' encounter with prey, this can be counterbalanced by more numerous and less vigilant prey. Finally, predation success is also influenced by the species-specific hunting modes of the predator and escape capabilities of the prey (VanLandeghem *et al.*, 2011; Ranåker *et al.*, 2012); both may be influenced by environmental state of the lake.

Large perch *Perca fluviatilis* L. 1758 are a common piscivorous predator in temperate freshwaters in the northern hemisphere. *Perca fluviatilis* has to go through ontogenetic life stages with possible bottlenecks to successfully become piscivorous at lengths of *c*. 15 cm total length (L_T) (Persson & Greenberg, 1990; Craig, 2000). Piscivorous *P. fluviatilis* are generally less abundant in hypereutrophic lakes compared with mesotrophic–eutrophic clear lakes (Jeppesen *et al.*, 2000). This can be attributed to the absence of submerged vegetation in hypereutrophic lakes, which is important for *P. fluviatilis* during several ontogenetic stages (Craig, 2000). The high turbidity in hypereutrophic lakes may also result in suboptimal feeding as vision provides the main source of sensory information in *P. fluviatilis* during search and encounter with prey fishes (Guthrie & Muntz, 1993; Craig, 2000). Growth limitation in earlier life stages of *P. fluviatilis*, due to lack of vegetation or intra or interspecific competition for invertebrates with the numerous young roach *Rutilus rutilus* (L. 1758) in hypereutrophic lakes, may explain the reduced recruitment to the piscivorous stage in nutrient-rich lakes with low-visibility environments (Persson & Greenberg, 1990).

Perca fluviatilis are group hunters known to hunt by actively chasing down their prey (Eklöv, 1992). They are capable of splitting up schools of prey fishes and hunting down individuals by cooperative group behaviour (Turesson & Brönmark, 2004). This cooperative group hunting is assisted by vision and is likely to be impaired in turbid water and hence is also likely to vary between lakes in different environmental states as well as within a lake during periods of varying water clarity.

The visual constraints and the lack of submerged vegetation provide good explanations why *P. fluviatilis* should be constrained in hypereutrophic conditions. Piscivorous *P. fluviatilis* can be found in nutrient-rich lakes, however, although typically in much lower density than in lakes with clear water (Jeppesen *et al.*, 2000). This raises the intriguing question: How can piscivorous *P. fluviatilis* cope with the apparent challenging conditions they face in hypereutrophic waters? The effect of turbidity on *P. fluviatilis* predation has frequently been explored for smaller individuals; *P. fluviatilis* predation success was reduced on fish in turbid water (Radke & Gaupisch, 2005; Pekcan-Hekim & Lappalainen, 2006). A recent mesocosm experiment of larger *P. fluviatilis*, however, showed that predation rate on prey fishes did not decrease significantly in turbid water (Jacobsen *et al.*, 2014). Likewise, other studies of related piscivorous species [yellow perch *Perca flavescens* (Mitchell, 1814) (Abrahams & Kattenfeld, 1997); largemouth bass *Micropterus salmoides* (Lacépède 1802) (Reid *et al.*, 1999)] have shown no effect of turbidity on predation rate. Turbidity affected *P. fluviatilis*, however, forage on prey from lower trophic levels to a variable degree (Granquist & Mattila, 2004; Nurminen *et al.*, 2010). Thus, it appears that poor light conditions impair the predation rate of large, piscivorous *P. fluviatilis* less than the feeding rate of smaller individuals feeding on other prey items. Previous field studies of piscivorous *P*.
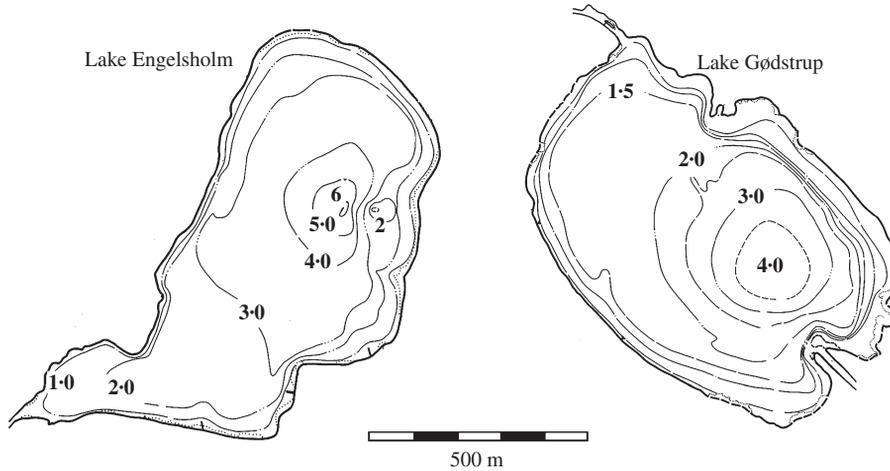
FIG. 1. Maps of the two study lakes: The mesotrophic Lake Engelsholm and the hypereutrophic Lake Gødstrup with depth isopleths.

fluviatilis behaviour were carried out in clear-water lakes (Imbrock *et al.*, 1996; Jacobsen *et al.*, 2002), whereas the few studies on larger *P. fluviatilis* and turbidity are based on laboratory or mesocosm approaches (Radke & Gaupisch, 2005; Jacobsen *et al.*, 2014), while no field studies of large *P. fluviatilis* behaviour in turbid, hypereutrophic conditions have been published.

The aim of this study was to examine large piscivorous *P. fluviatilis* behaviour in a hypereutrophic, turbid environment compared with a mesotrophic clear-water environment. This was performed in the field by the use of radio-telemetry where seasonal and diel patterns in activity and habitat choice were compared between *P. fluviatilis* in a lake with clear water and low prey density and a lake with turbid water and high prey density. Both lakes had no submerged vegetation. It was hypothesized that large *P. fluviatilis* in the hypereutrophic turbid lake have adopted an alternative behavioural strategy to meet the environmental constraints.

MATERIALS AND METHODS

STUDY AREAS

Both the two study lakes, Lake Engelsholm (55° 43′ 00″ N; 09° 19′ 00″ E) and Lake Gødstrup (56° 09′ 20″ N; 08° 54′ 20″ E), are located in the central part of Jutland, Denmark. Both lakes are rectangular in shape, 43 and 46 ha with mean depths of 2·6 m (maximum depth: 6·1 m) and 1·6 m (maximum depth: 4·0 m), respectively (Fig. 1). Lake Engelsholm (mean total P = 0·05 mg P l^{-1}) had Secchi disc depth between 3·0 and 3·5 m during the study period except in August 2006, where Secchi depth decreased briefly to 1·7 m. In Lake Gødstrup (mean total P = 0·36 mg P l^{-1}), Secchi disc depth was <0·4 m during summer and 0·6–0·8 m in winter. According to Secchi depth, Lake Engelsholm is classified as mesotrophic and Lake Gødstrup as hypereutrophic (Carlson & Simpson, 1996). The study lakes were selected to ensure that their physical characteristics were as similar as possible, except for water clarity, which was expected to be a prominent driver of variation in *P. fluviatilis* behaviour (Bergman, 1988) along with differences in fish composition or density. Standardized fish surveys with gillnets in Lake

TABLE I. Number of tagged large *Perca fluviatilis* during each tracking session

	Dates for tracking sessions					
Lake Engelsholm	June 2006 13−14	June 2006 26−27	October 2006 26−17	November 2006 6−7	March 2007 28−29	May 2007 8−9
Number of tagged fish	20	18	22	22	15	9
Lake Gødstrup	June 2006 14−15	June 2006 27−28	October 2006 24−25	November 2006 13−14	March 2007 27−28	May 2007 9−10
Number of tagged fish	20	20	20	19	16	10

Engelsholm (Jensen & Müller, 2006) and Lake Gødstrup (S. Berg, unpubl. data) showed that the dominant species in both lakes were *P. fluviatilis*, *R. rutilus*, pike *Esox lucius* L. 1758, bream *Abramis brama* (L. 1758), ruffe *Gymnocephalus cernua* (L. 1758) and European eel *Anguilla anguilla* (L. 1758). The density of fishes varied and the density of fishes <10 cm L_T, especially *R. rutilus* (potential prey for larger *P. fluviatilis*), was higher in hypereutrophic Lake Gødstrup [*R. rutilus* 159·3 catch per unit of effort (CPUE; individuals per gillnet night); *P. fluviatilis* 18·1 CPUE] than in mesotrophic Lake Engelsholm (*R. rutilus* 6·0 CPUE; *P. fluviatilis* 61·1 CPUE). In contrast to the interlake variation in water clarity and density of smaller fishes, there was no difference in abundance of submerged macrophytes which were almost absent in both lakes. Floating leaved *Persicaria amphibia* and emergent vegetation, however, occurred along the shoreline of Lake Engelsholm and in Lake Gødstrup floating leaved *Nuphar lutea* covered a small part of the littoral zone outside the abundant emergent vegetation (pers. obs.).

CAPTURE AND RADIO-TAGGING

In May 2006, 20 *P. fluviatilis* from Lake Engelsholm and 20 *P. fluviatilis* from Lake Gødstrup were tagged with radio-transmitters (Model F1585, Advanced Telemetry Systems Inc.; www.atstrack.com; flat shaped, length 2 cm, mass in air 2·8 g, <1% of body mass of all tagged *P. fluviatilis*). To study autumn and winter behaviour, 20 *P. fluviatilis* from Lake Engelsholm and 15 *P. fluviatilis* from Lake Gødstrup were caught and tagged in September 2006 to supplement those tagged *P. fluviatilis* from May whose tags were still transmitting. Another five fish were tagged in March 2007 in Lake Gødstrup to ensure enough data for the last tracking sessions.

In both lakes, *P. fluviatilis* for tagging were caught by gillnetting and electrofishing and held in 4 m × 4 m enclosures near the lake shore until tagging at a maximum of 24 h later. Individual fish were anaesthetized in a 60 mg l^{-1} solution of eugenol (Javahery *et al.*, 2012). The *P. fluviatilis* were measured (L_T), weighed and then placed on a surgical support pillow. The transmitter was inserted into the body cavity through a mid-ventral 10−15 mm incision, anterior to the pelvic girdle. The antenna was run through a separate hole from the body cavity, pierced with a blunt needle posterior to the incision. The incision was closed with one to two separate viacryl absorbable sutures. The complete tagging was carried out within 3−5 min while the fish was kept partly in water and the gills were regularly flushed with fresh water. After tagging, the *P. fluviatilis* recovered from anaesthesia in tanks with aerated lake water for 10−15 min. After recovery, the *P. fluviatilis* were released in the lake close to the shore at the tagging location.

Nine to 22 *P. fluviatilis* (mean ± S.D. L_T = 32·4 ± 1·7 cm, range: 29·8−36·2 cm; mean ± S.D. mass, M = 429·8 ± 63·2 g, range: 326−594 g) were included in the analysis for Lake Engelsholm for each period (Table I). In Lake Gødstrup, between 10 and 20 fish (mean ± S.D. L_T = 33·9 ± 4·2 cm, range: 29·0−42·5 cm; mean ± S.D. M = 535 ± 222 g, range: 288−1094 g) were represented in the tracking (Table I). The unequal number of fish during periods was due to transmitter malfunction and mortality of tagged *P. fluviatilis*: One fish was found dead shortly after tagging, and in total 10 individuals out of 80 tagged fish were assumed dead after 2−5 months. The low number of fish in May was due to transmitters running out of power.

TRACKING

Movement and habitat use of the tagged *P. fluviatilis* were studied by manually tracking each individual in relation to four key times of day: midday, sunset, midnight and sunrise. During each 24 h tracking session, each fish was positioned *c.* 75 min before and 75 min after each of the four key times of day, resulting in *c.* 2·5 h (mean ± S.D. Lake Engelsholm: 2·38 ± 0·49 h; Lake Gødstrup: 2·35 ± 0·51 h) between two consecutive positions. The 24 h tracking sessions were carried out six times in each lake (see Table I). The short time interval between sunset and sunrise in June made it necessary to combine the two trackings after sunset and before midnight to one, resulting in seven locations in June instead of the usual eight per session. Tracking sessions in the two lakes always took place on two successive days (Table I). Tracking of the fish was performed from a small boat with an outboard 4 HP engine using a hand-held Yagi antenna. The position of each individual, along with the time of tracking, was stored on a handheld GPS-unit (Garmin GPSMAP 76, Garmin International Inc.; www.garmin.com). During tracking sessions, daytime water temperature and Secchi depth were measured.

For each tracking session, the eight (seven in June) positions of each fish were used to calculate four minimum activity measures according to time of day (TOD) (around midday, sunset, midnight and sunrise, respectively). Activity was calculated as the displacement between the two positions in m moved h^{-1}, using the exact times of the location. Tracking sessions were assigned to summer (May, June and June) or winter (October, November and March).

Distance to shoreline at each position was used as a proxy of habitat use, indicating the degree of pelagic or open water residence, since none of the lakes had any extended vegetated littoral zone, *i.e.* beds of submerged macrophytes. To illustrate day and night habitat use, means of the two midday locations and the two midnight locations were compared.

DIET ANALYSIS AND CONDITION

Values of L_T and M were used to calculate Fulton's condition factor (K) (Fulton, 1904; Weatherley & Rogers, 1978) for *P. fluviatilis* in both lakes using measurements from both tagged individuals and individuals caught for diet analysis. *Perca fluviatilis* for diet analysis were sampled in both lakes in June and September 2006 by gillnetting between 1000 and 1400 hours, leaving the nets for a maximum of 2 h. *Perca fluviatilis* for diet analysis were in the same L_T range as the tagged individuals (Lake Engelsholm: mean ± S.D. = 31·9 ± 2·2 cm, range: 25·4−36·8 cm, $n = 68$; Lake Gødstrup: mean ± S.D. = 34·9 ± 4·1 cm, range: 25·5−43·2 cm, $n = 44$). *Perca fluviatilis* were euthanized by a lethal dose of benzocaine (Jepsen *et al.*, 2001) following permission number 2012-DY-2934-00007. Stomachs were removed and preserved in 70% ethanol for later analysis. In the laboratory, stomach content was analysed to family level for invertebrates and to species level for fishes. Frequency of occurrence of each prey group, invertebrates and fishes, as well as empty stomachs was assessed.

STATISTICS

Activity levels were analysed using a linear mixed effect (LME) modelling approach (Pinheiro & Bates, 2000; Zuur *et al.*, 2009) to examine whether the observed data could be explained by the following variables: TOD, lake, season, L_T and K. Fish ID was entered as a random component to account for the repeated measures obtained from each individual. TOD, lake and season were entered as categorical variables and included in the starting model as a three-way interaction, including all two-way interactions and main effects. L_T and K were entered as covariates and included as a main effect in the starting model. Activity levels were $\log_{10}$ transformed prior to modelling to meet model assumptions of normality.

To analyse whether mean distances to the shoreline varied between TOD, season and lake, a similar LME model was applied. The response variable was square-root transformed to ensure that model assumptions of normality were met.

Model reduction for both activity levels and distance to shore were carried out following Pinheiro & Bates (2000) and Zuur *et al.* (2009) using the likelihood ratio test to compare nested models. Non-significant (at the $P = 0.05$ level) model terms were removed. The models were validated by visual inspection of residuals to assure that model assumptions of homogeneity of variance, normality and independence were met.

TABLE II. Summary and output for linear mixed effect (LME) statistical model to analyse the activity patterns (Act) of *Perca fluviatilis*

Summary of fixed, random (A) and variance (B) terms in the optimal model

Response	Model term	d.f.	L-ratio	P
Log_{10} (Act)	Lake × TOD × season	3	18·39	<0·001
	Fish ID (A)	1	19·56	<0·001
	TOD × season (B)	7	17·66	<0·05

Model output for the optimal model

	Value	S.E.	d.f.	t-value	P-value
(Intercept)	1·20	0·08	737	14·29	<0·001
Lake 2	−0·02	0·12	75	−0·18	>0·05
TOD 2	0·55	0·10	737	5·38	<0·001
TOD 3	−0·44	0·10	737	−4·28	<0·001
TOD 4	0·53	0·11	737	4·72	<0·001
Season 2	0·25	0·11	737	2·34	<0·05
Lake 2 × TOD 2	−0·22	0·14	737	−1·53	>0·05
Lake 2 × TOD 3	0·81	0·14	737	5·68	<0·001
Lake 2 × TOD 4	−0·08	0·16	737	−0·54	>0·05
Lake 2 × season 2	−0·32	0·15	737	−2·16	<0·05
TOD 2 × season 2	−0·25	0·14	737	−1·79	>0·05
TOD 3 × season 2	−0·12	0·13	737	−0·93	>0·05
TOD 4 × season 2	−0·32	0·14	737	−2·34	<0·05
Lake 2 × TOD 2 × season 2	0·12	0·20	737	0·62	>0·05
Lake 2 × TOD 3 × season 2	−0·45	0·18	737	−2·45	<0·05
Lake 2 × TOD 4 × season 2	0·26	0·20	737	1·32	>0·05

Lake 2, Lake Gødstrup (compared with Lake 1); TOD, time of day: TOD 2, midday; TOD 3, sunset; TOD 4, midnight; season 2, winter. Numbers refer to comparisons with lower numbers, f.x TOD 3 means difference between TOD 3 and TOD 2 and TOD 1.

The L_T of all captured *P. fluviatilis* as well as K-values of fish of same size range (29–36 cm) were compared between lakes in *t*-tests. The L_T was ln transformed to meet the assumption of normality and homogeneity of variance. Between-lake differences in diets were tested using χ^2 tests.

Statistical analyses were performed using R (R Development Core Team; www.r-project.org) and the nlme package (Pinheiro *et al.*, 2012).

RESULTS

Activity patterns of *P. fluviatilis* differed between the two lakes (Fig. 2). The optimal LME model describing the activity showed a three-way interaction between Lake, TOD and season that was highly significant. The optimal LME model allowed for unequal variance per TOD × season stratum (Table II and Fig. 2). The L_T and K were non-significant (L_T, d.f. = 1, L-ratio < 0·001; $P > 0·05$; K, d.f. = 1, L-ratio < 1·69, $P > 0·05$) and therefore not included in the optimal model.
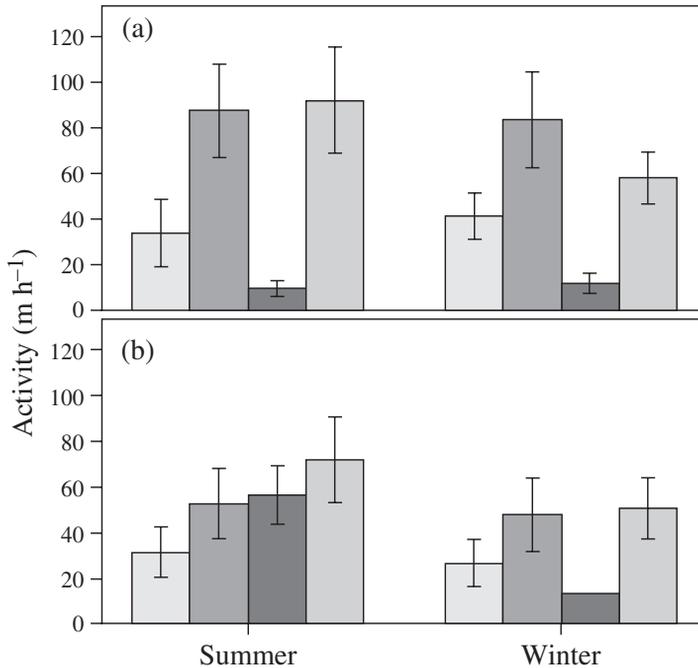
FIG. 2. Minimum activity levels (mean ± S.E.) during midday (□), sunset (▨), midnight (■) and sunrise (□) for *Perca fluviatilis* in the (a) mesotrophic lake and (b) hypereutrophic lake during summer and winter.

The significant three-way interaction between TOD, lake and season indicates a complex relation between *P. fluviatilis* activity and these three variables. The interaction indicates that each of these variables did influence *P. fluviatilis* activity but this effect was dependent on the other two variables. For instance, as seen in Fig. 2, there was a clear effect of TOD, but the magnitude and direction of this effect depended on both season and lake. In the mesotrophic lake, there were explicit activity peaks during morning and sunset, which were not apparent in the hypereutrophic lake. Activity was very low during the night in the mesotrophic lake, but continued during the night in the hypereutrophic lake. This difference between lakes disappeared in winter when diel activity variation was more alike in the two lakes, and activity peaks during morning and sunset occurred (Fig. 2).

Distance to the shore followed the same variations (Fig. 3). The mixed model revealed a significant three-way interaction between lake, TOD and season (Table III). In the mesotrophic lake, *P. fluviatilis* were mostly pelagic during daytime and littoral during night in summer, whereas the opposite pattern was seen in the hypereutrophic lake, where *P. fluviatilis* tended to be closer to the shore during the daytime than during the night (Fig. 3). This pattern changed during winter, where *P. fluviatilis* in both lakes were more pelagic during daytime and closer to the shore during night (Fig. 3). The L_T had a positive relation to distance to the shore (Table III), indicating that larger *P. fluviatilis* were more pelagic. K did not significantly influence distance to the shore (d.f. $=1$, L-ratio < 0.25, $P > 0.05$) and was therefore excluded from the final model.
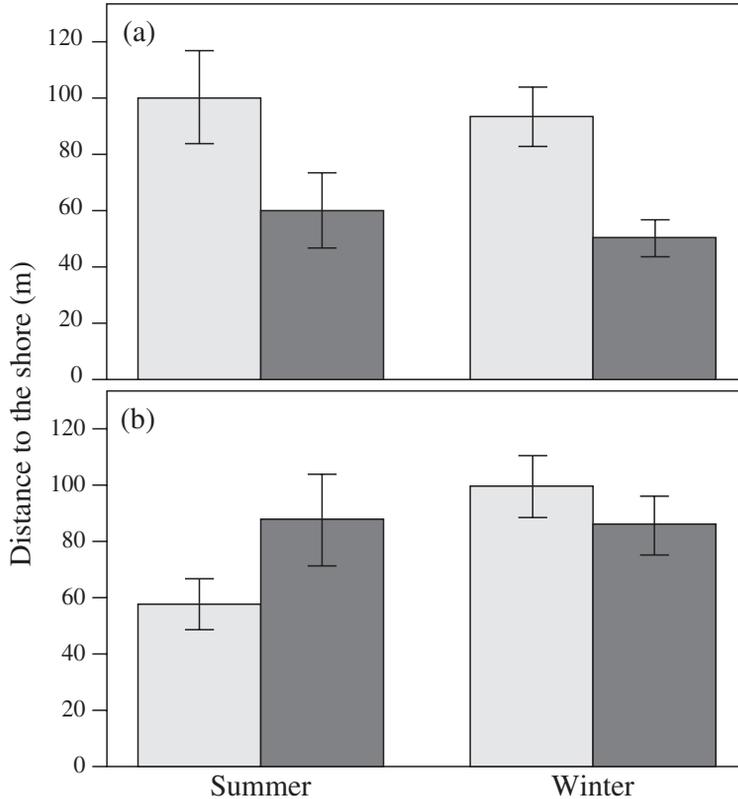
FIG. 3. Habitat use and pelagic residence (mean ± S.E. distance to the shore) of *Perca fluviatilis* during midday (☐) and midnight (■) in the (a) mesotrophic lake and (b) hypereutrophic lake during summer and winter.

DIET AND CONDITION FACTORS

Perca fluviatilis caught for tagging and stomach analysis were largest in the hypereutrophic lake (*t*-test, d.f. = 192, $P < 0.001$) compared with the mesotrophic lake. The K of *P. fluviatilis* of similar L_T range (29–36 cm) in the mesotrophic lake (mean ± S.D. $K = 1.25 \pm 0.07$, $n = 108$) and the hypertrophic lake (mean ± S.D. $K = 1.29 \pm 0.10$, $n = 86$) were not significantly different (*t*-test, d.f. = 155, $P > 0.05$), but with a tendency to better condition in the hypereutrophic lake.

There were significant between-lake differences in diet in both June and September for most prey groups and number of empty stomachs $\left(\chi^2_1,\right)$ $P < 0.001$ except for invertebrates in September ($P > 0.05$) and empty stomachs in June ($P > 0.05$) (Fig. 4). The diet of *P. fluviatilis* in the mesotrophic lake was dominated by chironomids in June and by fishes in September (Fig. 4) with a share of empty stomachs of 12% in June and 65% in September. In total, 78% of the prey fishes were small ($L_T = 45$–97 mm) *P. fluviatilis* and 22% were small ($L_T = 45$–75 mm) *R. rutilus*. In the hypereutrophic lake, *P. fluviatilis* were mainly consuming fish prey in both June and September with a share of empty stomachs of 23% in June and 6% in September (Fig. 4). The prey fishes here were 88% small *R. rutilus* ($L_T = 27$–100 mm) and 12% small *P. fluviatilis* ($L_T = 27$–162 mm).

TABLE III. Summary and output for linear mixed effect (LME) statistical model to analyse the effect of lake, time of day (TOD) and season on *Perca fluviatilis* distance to the shore (see Table II)

Summary of fixed, random (A) and variance (B) terms in the optimal model

Response	Model term	d.f.	*L*-ratio	*P*-value
sqrt (distance)	Lake × TOD × season	1	7·55	<0·01
	L_T	1	3·91	<0·05
	Fish ID (A)	1	140·11	<0·001
	TOD × season (B)	3	24·25	<0·001

Model output for the optimal model

	Value	S.E.	d.f.	*t*-value	*P*-value
Intercept	4·32	2·32	663	1·86	>0·05
Lake 2	−2·24	0·57	94	−3·92	<0·001
TOD 2	−1·82	0·44	663	−4·14	<0·001
Season 2	0·63	0·45	663	1·42	>0·05
L_T	0·14	0·07	94	1·96	>0·05
Lake 2 × TOD 2	3·88	0·62	663	6·30	<0·001
Lake 2 × season 2	2·26	0·61	663	3·72	<0·001
TOD 2 × season 2	−0·58	0·56	663	−1·03	>0·05
Lake 2 × TOD 2 × season 2	−2·16	0·79	663	−2·75	<0·01

L_T, total length.

DISCUSSION

Previous studies of *P. fluviatilis* behaviour in natural settings were conducted in clear-water lakes (Imbrock *et al.*, 1996; Jacobsen *et al.*, 2002; Zamora & Moreno-Amich, 2002), whereas knowledge of how larger piscivorous *P. fluviatilis* behave under eutrophic or hypereutrophic conditions in turbid water is scarce (Radke & Gaupisch, 2005; Jacobsen *et al.*, 2014) and has not been studied in the field. In this study, large *P. fluviatilis* appeared to adopt a different behaviour in a hypereutrophic turbid lake during summer, compared with a mesotrophic lake, being moderately active during the entire diel cycle. Hence, in contrast to *P. fluviatilis* in the mesotrophic lake, the individuals in the hypereutrophic lake had no explicit crepuscular feeding pattern with activity peaks at sunrise and sunset. The more moderate, but continuing, activity in the hypereutrophic lake was linked to a choice of pelagic and dispersed habitat during both day and night, whereas *P. fluviatilis* in the mesotrophic lake were most pelagic during daytime and in general stayed closer to the littoral zone during night, concomitant with a low activity level.

Perca fluviatilis had similar condition factors and were able to consume fish prey in both lakes. Hence, there are no indications that *P. fluviatilis*, within the size span investigated here, experienced reduced feeding conditions in the hypereutrophic turbid lake in this study. This suggests that variation in behaviour between the two lakes could represent alternative strategies coping equally well with the different environmental constraints and prey densities the two lakes represent.
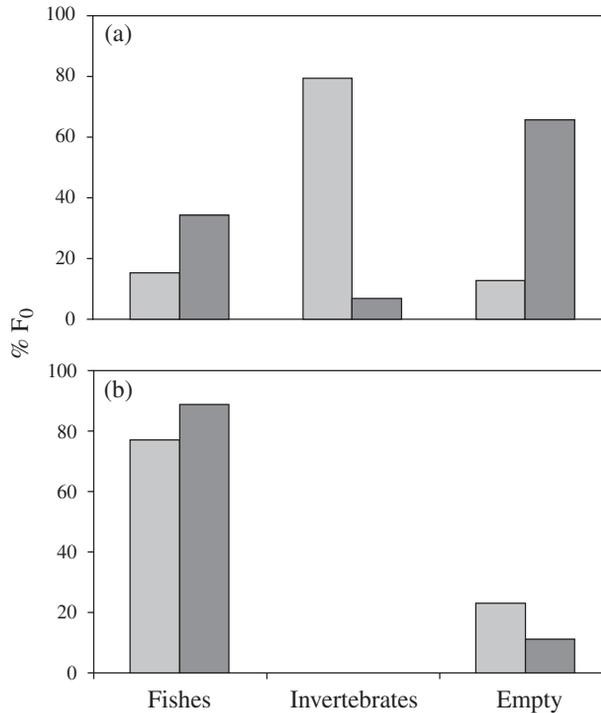
FIG. 4. Diet choice (per cent frequency of occurrence, $\%F_O$) of *Perca fluviatilis* in the (a) mesotrophic lake and (b) hypereutrophic lake in June (□) and September (■).

INTERLAKE VARIATION RELATED TO WATER VISIBILITY AND PREY DENSITIES

Non-spawning related activity is in general interpreted as foraging time for non-migratory active predatory fishes (Kerr, 1982), and likewise in the following it is assumed that the activity observed is linked (mainly) to foraging. Hence, these results suggest that during summer large *P. fluviatilis* in the hypereutrophic lake were foraging during extended periods including night, although with lower average movements during dawn and dusk compared with the large individuals in the mesotrophic lake.

Low visibility decreases the reaction distance of both predator and prey (Ranåker *et al.*, 2012). The outcome of a predator–prey encounter depends on the match of predator strike distance and prey escape distance. Hunting mode depends on reaction distance and for a cruising predator such as *P. fluviatilis*, reaction distance in the turbid hypereutrophic lake may have been too short to allow for active hunting bursts, once prey was detected, *i.e.* running the prey down over a distance, as is the typical *P. fluviatilis* hunting strategy in clear water (Eklöv & Diehl, 1994). Hence, it is speculated that if active hunting bursts were impaired in the low visibility in the hypereutrophic lake, large *P. fluviatilis* may have adopted a more moderate cruising behaviour, accidentally encountering prey at a short distance. This could explain the uniform foraging pattern in the hypereutrophic lake, and also explain the fact that *P. fluviatilis* were active at night in this lake in contrast to the results from other studies of diel rhythms of this species (Bergman, 1988; Craig, 2000; Jacobsen *et al.*, 2002). In this study, minimum

activity was measured as the distance between two positions with a 2·5 h interval, which did not enable us to reveal actual speed of hunting and therefore to conclude whether crepuscular activity peaks in the mesotrophic lake actually reflected a period of active hunting runs.

Gillnet surveys in both lakes revealed that the density of prey fishes, especially *R. rutilus*, were considerably higher in the hypereutrophic lake, which possibly have assisted the foraging success of large *P. fluviatilis* (Jensen & Müller, 2006; S. Berg, unpubl. data). Thus, increased prey density may have compensated visual foraging constraints in the hypereutrophic lake. This idea is supported by a recent mesocosm experiment where large *P. fluviatilis* increased consumption rate with increased prey fish density regardless of turbidity (Jacobsen *et al.*, 2014). High prey density in turbid waters did not compensate for the reduced reaction distance for a visually hunting sit-and-wait predator (*E. lucius*) (Turesson & Brönmark, 2007), although these authors measured encounters but not consumption.

SPATIAL AND TEMPORAL CO-OCCURRENCE OF PREY AND PREDATORS

At a first glance, the higher prey density in the hypereutrophic lake does not explain the difference in *P. fluviatilis* activity pattern in the two lakes, but interlake behavioural differences of both prey and large *P. fluviatilis* may explain the difference. Crepuscular feeding in the mesotrophic lake in this study, as observed in previous studies of *P. fluviatilis* behaviour in clear-water habitats (Craig, 1977; Alabaster & Stott, 1978; Jacobsen *et al.*, 2002), could be explained by *P. fluviatilis* feeding during a short effective period being sufficient to get enough food. Crepuscular activity, however, could also indicate temporary access to the preferred prey. In clear water, prey fishes are likely to move to the open water during dusk and back to the littoral zone at dawn (Bohl, 1980; Gliwicz & Jachner, 1992; Jacobsen *et al.*, 2004) rendering these periods optimal for hunting. This anti-predator behaviour is abandoned in turbid water (Abrahams & Kattenfeld, 1997; Jacobsen *et al.*, 2004; Snickars *et al.*, 2004) where prey fishes are more active and dispersed over the entire lake (Jacobsen *et al.*, 2004), resulting in higher accessibility in open water during the entire diel cycle. These behavioural patterns were confirmed by a co-study of prey fish distribution in the two study lakes (Andersen, 2007). Scattered prey-fish distribution in hypereutrophic turbid lakes coincide with a dispersed distribution of large *P. fluviatilis* in the hypereutrophic study lake during both day and night; hence, large *P. fluviatilis* are likely to interact with prey and their spatial and temporal distribution or *vice versa*.

Large *P. fluviatilis* might themselves be susceptible to predation from other piscivorous fishes or birds, *e.g. E. lucius* or cormorant *Phalacrocorax carbo sinensis*; in both lakes, there was a population of large *E. lucius*. Shorter activity peaks and less activity during midday avoiding proximity to the littoral zone, a preferred clear-water habitat for *E. lucius* (Chapman & Mackay, 1984; Andersen *et al.*, 2008), may be a strategy to limit the risk of predation for large *P. fluviatilis* in the mesotrophic lake.

Competition is another factor that could add to behavioural variation between the two study lakes. Based on the density of prey fishes, which is highest in the hypereutrophic lake, it could be argued that the *P. fluviatilis* in the mesotrophic lake face higher competition regimes. Unfortunately, lack of data on the density of competitors (large *P. fluviatilis* and *E. lucius*) in the two lakes, limits conclusions on the role of competition in shaping the observed behavioural patterns.

DIEL ACTIVITY AND SEASONAL CHANGES

During winter, diel activity patterns in the hypereutrophic lake changed towards a crepuscular activity pattern as night activity subsided. The reason for this change is not clear. Secchi depth was higher during winter, but still below 0·8 m. Whether this increase in visibility during daylight hours was enough to change foraging strategy is dubious; however, decreased metabolic needs in the cooler water during winter might have made it sufficient to be active during crepuscular periods.

The general activity level did not change in the mesotrophic lake in winter but appeared to be lowered in the hypereutrophic lake. Even though fishes have a lower metabolic rate during winter (Fry 1971), many fishes remain rather active and not as passive as previously thought (Jepsen *et al.*, 1999; Salonen *et al.*, 2009; Baktoft *et al.*, 2012). Jacobsen *et al.* (2002) found *P. fluviatilis* activity level in a clear-water lake to remain high in winter, but concentrated on fewer daylight hours; thus, activity per active hour increased.

This study suggests that *P. fluviatilis* established themselves as piscivores in a nutrient-rich lake with turbid water, by adopting alternative strategies to successive feeding, probably assisted by a high prey-fish density. It is acknowledged that this study is based on a limited number of lakes. Additional studies is suggested to show how large piscivorous *P. fluviatilis*, which often play an important structuring role in European temperate lowland lakes (Jeppesen *et al.*, 2000), cope with varying environmental conditions. It is believed that the results presented here are a useful first step towards a better understanding of this.

References

Abrahams, M. & Kattenfeld, M. (1997). The role of turbidity as a constraint on predator–prey interactions in aquatic environments. *Behavioural Ecology and Sociobiology* **40**, 169–174.

Alabaster, J. S. & Stott, B. (1978). Swimming activity of perch, *Perca fluviatilis* L. *Journal of Fish Biology* **12**, 587–591.

Andersen, M. (2007). The effect of turbidity on prey fish behaviour in shallow temperate lakes. *Turbiditets indflydelse på adfærden hos søfisk*, pp. 28–44. MSc Thesis, University of Århus, Institute of Biology, Denmark. http://orbit.dtu.dk/en/publications/turbiditets-indflydelse-paa-adfaerd-hos-soefisk(ce019203-b8a3-47ff-b601-5d96271fd2c7).html/

Andersen, M., Jacobsen, L., Grønkjær, P. & Skov, C. (2008). Turbidity increases behavioural diversity in northern pike, *Esox lucius* L., during early summer. *Fisheries Management and Ecology* **15**, 377–384.

Baktoft, H., Aarestrup, K., Berg, S., Boel, M., Jacobsen, L., Jepsen, N., Koed, A., Svendsen, J. C. & Skov, C. (2012). Seasonal and diel effects on the activity of northern pike studied by high-resolution positional telemetry. *Ecology of Freshwater Fish* **21**, 386–394.

Bergman, E. (1988). Foraging abilities and niche breadths of two percids, *Perca fluviatilis* and *Gymnocephalus cernua*, under different environmental conditions. *Journal of Animal Ecology* **57**, 443–453.

Bohl, E. (1980). Diel pattern of pelagic distribution and feeding in planktivorous fish. *Oecologia (Berlin)* **44**, 368–375.

Carlson, R. E. & Simpson, J. (1996). *A Coordinator's Guide to Volunteer Lake Monitoring Methods*. Madison, WI: North American Lake Management Society.

Carpenter, S. R. & Kitchell, J. F. (1993). *The Trophic Cascade in Lakes*. Cambridge: Cambridge University Press.

Carter, M. W., Shoup, D. E., Dettmers, J. M. & Wahl, D. H. (2010). Effects of turbidity and cover on prey selectivity of adult smallmouth bass. *Transactions of the American Fisheries Society* **139**, 353–361.

Chapman, C. A. & Mackay, W. C. (1984). Direct observations of habitat utilization by northern pike. *Copeia* **1984**, 225–228.

Craig, J. F. (1977). Seasonal changes in the day and night activity of adult perch, *Perca fluviatilis* L. *Journal of Fish Biology* **11**, 161–166.

Craig, J. F. (2000). *Percid Fishes. Systematics, Ecology and Exploitation*. Oxford: Blackwell Science.

Eklöv, P. (1992). Group foraging versus solitary foraging efficiency in piscivorous predators: the perch, *Perca fluviatilis*, and pike, *Esox lucius*, patterns. *Animal Behavior* **44**, 313–326.

Eklöv, P. & Diehl, S. (1994). Piscivore efficiency and refuging prey: the importance of predator search mode. *Oecologia* **98**, 344–353.

Fry, F. E. J. (1971). The effect of environmental factors on the physiology of fish. In *Fish Physiology: Environmental Factors* (Hoar, W. S. & Randall, D. J., eds). New York, NY: Academic Press.

Fryxell, J. M. & Lundberg, P. (1998). *Individual Behaviour and Community Dynamics*. London: Chapman & Hall.

Fulton, T. W. (1904). The rate of growth of fishes. *22nd Annual Report of the Fisheries Board of Scotland* **1903**, 141–241.

Gliwicz, Z. M. & Jachner, A. (1992). Diel migrations of juvenile fish: a ghost of predation past or present? *Archiv für Hydrobiologie* **124**, 385–410.

Granquist, M. & Mattila, J. (2004). The effect of turbidity and light intensity on the consumption of mysids by juvenile perch (*Perca fluviatilis* L.). *Hydrobiologia* **514**, 93–101.

Guthrie, D. M. & Muntz, W. R. A. (1993). Role of vision in fish behaviour. In *Behaviour of Teleost Fishes* (Pitcher, T. P., ed.), pp. 89–121. London: Chapman & Hall.

Imbrock, F., Appenzeller, A. & Eckmann, R. (1996). Diel and seasonal distribution of perch in Lake Constance: a hydroacoustic study and in situ observations. *Journal of Fish Biology* **49**, 1–13.

Jacobsen, L. & Berg, S. (1998). Diel variation in habitat use by planktivores in field enclosure experiments: the effect of submerged macrophytes and predation. *Journal of Fish Biology* **53**, 1207–1219.

Jacobsen, L., Berg, S., Broberg, M., Jepsen, N. & Skov, C. (2002). Activity and food choice of piscivorous perch (*Perca fluviatilis*) in a eutrophic shallow lake, investigated by radio-telemetry. *Freshwater Biology* **47**, 2370–2379.

Jacobsen, L., Berg, S., Jepsen, N. & Skov, C. (2004). Does behaviour of roach (*Rutilus rutilus* L.) differ between shallow lakes of different environmental states? *Journal of Fish Biology* **65**, 135–147.

Jacobsen, L., Berg, S., Baktoft, H., Nilsson, P.-A. & Skov, C. (2014). The effect of turbidity and prey fish density on consumption rates of piscivorous Eurasian perch *Perca fluviatilis*. *Journal of Limnology* **73**, 1–5. doi: 10.4081/jlimnol.2014.837

Javahery, S., Nekoubin, H. & Moradlu, A. H. (2012). Effect of anaesthesia with clove oil in fish (review). *Fish Physiology and Biochemistry* **38**, 1545–1552. doi: 10.1007/s10695-012-9682-5

Jeppesen, E., Jensen, J. P., Søndergaard, M., Lauridsen, T. & Landkildehus, F. (2000). Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorous gradient. *Freshwater Biology* **45**, 201–218.

Jepsen, N., Koed, A. & Økland, F. (1999). The movements of pikeperch in a shallow reservoir. *Journal of Fish Biology* **54**, 1083–1093.

Jepsen, N., Davis, L. E., Schreck, C. B. & Siddens, B. (2001). The Physiological Response of Chinook Salmon Smolts to Two Methods of Radio-Tagging. *Transactions of the American Fisheries Society* **130**, 495–500.

Kerr, S. R. (1982). Estimating the energy budgets of actively predatory fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **39**, 371–379.

Miner, J. G. & Stein, R. A. (1996). Detection of predators and habitat choice by small bluegills: effects of turbidity and alternative prey. *Transactions of the American Fisheries Society* **125**, 97–103.

Nurminen, L., Pekcam-Hekim, Z. & Horppila, J. (2010). Feeding efficiency of planktivorous perch *Perca fluviatilis* and roach *Rutilus rutilus* in varying turbidity: an individual based approach. *Journal of Fish Biology* **76**, 1848–1855.

Pekcan-Hekim, Z. & Lappalainen, J. (2006). Effects of clay turbidity and density of pikeperch (*Sander lucioperca*) larvae on predation by perch (*Perca fluviatilis*). *Naturwissenschaften* **93**, 356–359.

Persson, L. & Greenberg, L. A. (1990). Juvenile competitive bottlenecks: the perch (*Perca fluviatilis*)-roach (*Rutilus rutilus*) interaction. *Ecology* **71**, 44–56.

Pinheiro, J. C. & Bates, D. M. (2000). *Mixed Effects Models in S and S-PLUS*. New York, NY: Springer.

Radke, R. J. & Gaupisch, A. (2005). Effects of phytoplankton-induced turbidity on predation success of piscivorous Eurasian perch (*Perca fluviatilis*): possible implications for fish community structure in lakes. *Naturwissenschaften* **92**, 91–94.

Ranåker, L., Jönsson, M., Nilsson, P. A. & Brönmark, C. (2012). Effects of brown and turbid water on piscivore–prey fish interactions along a visibility gradient. *Freshwater Biology* **57**, 1761–1768.

Reid, S. M., Fox, M. G. & Whillans, T. H. (1999). Influence of turbidity on piscivory in largemouth bass (*Micropterus salmoides*). *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 1362–1369.

Salonen, K., Lepparanta, M., Viljanen, M. & Gulati, R. D. (2009). Perspectives in winter limnology: closing the annual cycle of freezing lakes. *Aquatic Ecology* **43**, 609–616.

Snickars, M., Sandström, A. & Mattila, J. (2004). Antipredator behaviour of 0 + year *Perca fluviatilis*: effects of vegetation density and turbidity. *Journal of Fish Biology* **65**, 1604–1613.

Turesson, H. & Brönmark, C. (2004). Foraging behaviour and capture success in perch, pikeperch and pike and the effects of prey density. *Journal of Fish Biology* **65**, 363–375.

Turesson, H. & Brönmark, C. (2007). Predator–prey encounter rates in freshwater piscivores: effects of prey density and water transparency. *Oecologia* **153**, 281–290.

Utne-Palm, A. C. (2002). Visual feeding of fish in a turbid environment: physical and behavioural aspects. *Marine and Freshwater Behaviour and Physiology* **35**, 111–128.

VanLandeghem, M. M., Carey, M. P. & Wahl, D. H. (2011). Turbidity-induced changes in emergent effects of multiple predators with different foraging strategies. *Ecology of Freshwater Fish* **20**, 279–286.

Weatherley, A. H. & Rogers, S. C. (1978). Some aspects of age and growth. In *Ecology of Freshwater Fish Production* (Gerking, S. D., ed.), pp. 52–74. Oxford: Blackwell Scientific Publications.

Zamora, L. & Moreno-Amich, R. (2002). Quantifying the activity and movement of perch in a temperate lake by integrating acoustic telemetry and a geographic information system. *Hydrobiologia* **483**, 2009–2218.

Zuur, A. F., Ieno, E. N., Walker, N. J., Anatoly, A. S. & Smith, G. M. (2009). *Mixed Effects Models and Extensions in Ecology with R*. New York, NY: Springer.

Electronic References

Jensen, H. & Müller, J. P. (2006). Notat om fiskene i Engelsholm Sø 2005. *Report from Fiskeøkologisk Laboratorium, Denmark*. Available at http://130.226.135.83/soerMap/getInfo.php?action=getReport&repId=1251/ (last accessed 18 November 2014).

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Development Core Team (2012). *nlme: Linear and Nonlinear Mixed Effects Models*. Available at http://cran.r-project.org/web/packages/nlme/index.html/