

Movement of a South American perch *Percichthys trucha* in a mountain Patagonian lake during spawning and prespawning periods

L. BURIA*†, S. J. WALDE‡, M. BATTINI†, P. J. MACCHI†,
M. ALONSO†, D. E. RUZZANTE‡ AND V. E. CUSSAC*†§

*Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina,

†Centro Regional Universitario Bariloche, Universidad Nacional del Comahue,
Quintral 1250 Bariloche, 8400 Río Negro, Argentina and ‡Department of Biology,
Dalhousie University, Halifax, NS, B3H 4J1 Canada

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Movement of the South American perch *Percichthys trucha* (Perciformes: Percichthyidae) was studied in a set of interconnected mountain lakes in northern Patagonia. Fish were tracked using attached acoustic tags and a fixed hydrophone array over two seasons, corresponding to the spawning (1999) and prespawning periods (2000). *Percichthys trucha* was found to move throughout the lake system, and to use a small, shallow, connected lake as a principal spawning area. In addition, detailed behavioural information was obtained for the spawning period. Most fish spent the initial 2 weeks descending from the littoral zone to depths of 5–8 m, presumably while feeding. Fish changed depth slowly, spending several days at each depth, and moving throughout the lake. A few days prior to the full moon, there was a change in behaviour thought to be associated with spawning, where the fish moved toward the vegetated littoral areas. Marked daily behaviour also began at this time, with movement to particular near-shore locations at dusk, and return to slightly greater depths offshore at or before dawn. Study of the behaviour of *P. trucha* during the breeding season has highlighted the conservation significance of the main locations within the lake system.

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INTRODUCTION

Percoids (perches and temperate basses) are frequently an important component of temperate lake fish communities (Moyle & Cech, 1982; Johnson, 1993; Nelson, 1994). Many northern hemisphere studies have demonstrated their influence on the composition and dynamics of fish communities through competition and predation (Sandheinrich & Hubert, 1984; Persson *et al.*, 2003). Much less is known about the ecology and behaviour of members of the family

§Author to whom correspondence should be addressed. Tel.: +54 02944 423374; fax: +54 02944 422111; email: vcussac@crub.uncoma.edu.ar

Percichthyidae, the southern hemisphere temperate lake equivalent. The Percichthyidae are found in Australia and in the Patagonian region of South America; their closest northern hemisphere freshwater relatives are probably the Moronidae (Johnson, 1993). In the temperate lakes of Patagonia, the Percichthyidae are represented by two genera (*Percichthys* Girard 1855 and *Percilia* Girard 1855). *Percilia* comprises two species, both of which occur only to the west of the Andes (Dyer, 2000). Five extant species have been described for *Percichthys* based on morphological differences (Ringuelet *et al.*, 1967), one of which, *Percichthys trucha* (Valenciennes 1833), is distributed throughout Patagonia (Arratia, 1983) and is usually the only species of the complex present in upper mountain lakes.

This study adds to the body of ecological and behavioural knowledge for *P. trucha* by using acoustic telemetry to examine the movement patterns of individual fish during the spawning and prespawning periods in the spring of two consecutive years. Transmitters were attached to individual fish, and signals were recorded by hydrophones placed at strategic locations in the water body. Fish were continuously tracked over periods of up to 2 months, allowing for the collection of a great deal of detailed behavioural information, but for a limited number of individuals. The study was conducted in a mountain lake system in north-western Patagonia (Argentina), consisting of three interconnected lakes: East and West Moreno, and Morenito. In the first year, movements and habitat use of 10 *P. trucha* were followed during the breeding season in the small Lake Morenito, where spawning was suspected to occur. In the following year, 10 fish were tracked in the larger Lake Moreno system during the period leading up to reproduction. The objectives of this study were to describe the behaviour of *P. trucha* in Lake Morenito during the spawning season, and to determine its range of movement in Lake Moreno during the pre-reproductive period. Specific goals were to determine (1) which zones of Lake Morenito (locations or depths) receive concentrated activity during the spawning season, (2) if temporal variation in activity corresponds to the lunar cycle and (3) if there is a daily pattern to activity during the spawning season.

MATERIALS AND METHODS

STUDY SITE

The study was conducted in the Lake Moreno system, located in the mountains of northern Patagonia (41°02' S; 71°32' W) (760 m altitude) (Fig. 1), and draining into Lake Nahuel Huapi, which drains into the Limay River. The system consists of two relatively large and connected lakes (East and West Moreno, 5.42 and 5.22 km² surface area respectively), a smaller lake (Morenito, 0.82 km² area) connected to the larger lakes by a shallow channel open from mid autumn to late spring, and an even smaller pond, Lake Ezquerra, which drains into Lake Morenito (Fig. 1). East and West Moreno are deep (c. 100 m), ultra-oligotrophic lakes (conductivity of 37 µS cm⁻¹). Both have some littoral areas, with pondweeds [*Schoenoplectus californicus* (Meyer) Soják and *Potamogeton linguatus* Hangström] in the shallows and the macrophyte, *Nitella* sp. in deeper waters. Lake Morenito is shallow (c. 15 m maximum depth), has higher conductivity (68 µS cm⁻¹), and aquatic plants are present in most of the littoral zone.

Percichthys trucha shares the Lake Moreno system with four other native species [*Galaxias maculatus* (Jenyns, 1842), *Galaxias platei* Steindachner, 1898, *Odontesthes hatcheri*

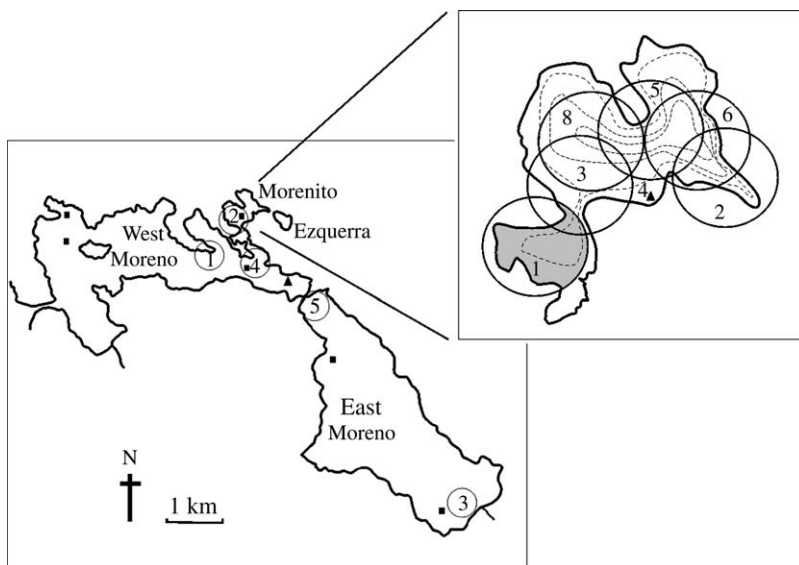


FIG. 1. The Lake Moreno system (41°02' S; 71°32' W; 760 m a.s.l.). Catch sites (■), release sites of tagged fish (▲), location and estimated recording area (○, 600 m diameter) of VR1 receivers (Arabic numeral) are indicated. The channel linking Lake Morenito to the larger lakes is shaded.

(Eigenmann, 1909) and *Diplomystes viedmensis* MacDonagh 1931], and with three exotic salmonids [*Salvelinus fontinalis* (Mitchill, 1814), *Oncorhynchus mykiss* (Walbaum, 1792) and *Salmo trutta* L. 1758]. However, *D. viedmensis* and *S. trutta* are rare (neither was captured in Lake Moreno during this study), and the other salmonids also show low abundances (*O. mykiss* is more common than *S. fontinalis*).

TRACKING

Fish were tracked over two 2 month periods (September to November): (1) within Lake Morenito in 1999, and (2) in the entire Lake Moreno system in 2000. Both studies were conducted during the months September to November, but due to interannual differences in water temperature, the 1999 trial encompassed the peak reproductive period, while the 2000 trial began before the majority of the fish had mature gonads. The studies were terminated just before the beginning of the sport fishery season (November 15) to avoid vandalism.

For the first trial, 10 healthy adult individuals were selected from the fish caught in Lake Morenito in winter (August 1999), as part of a seasonal sampling programme. Gillnets were set at 0 and 10 m depth and inspected hourly so that fish could be removed in good condition. The fish were transported 15 km to a large outdoor tank at the Universidad Nacional del Comahue, Bariloche hatchery, given prophylactic treatments [malachite green (1:500 000, 1 h with flow stopped)], but not fed. After 1 week, the fish were anaesthetized with benzocaine and weighed. Fish could be identified as ripe males in some cases, when light pressure caused the release of sperm. An ultrasonic transmitter V16P (VEMCO, 1998a) was suspended in an anterior-ventral position following Claireaux & Lefrançois (1998). The transmitter was attached by its handle to the articulation between preopercular and opercular bones and by the posterior part of the main transmitter body to the pelvic girdle (Fig. 2) using nylon monofilament (0.5 mm diameter) and a suture needle. The procedure took *c.* 5 min. The fish were returned to the tank and appeared to recover within 10 min. Fish were maintained in the tanks for another week to ensure that they were healthy, then lightly anaesthetized to switch

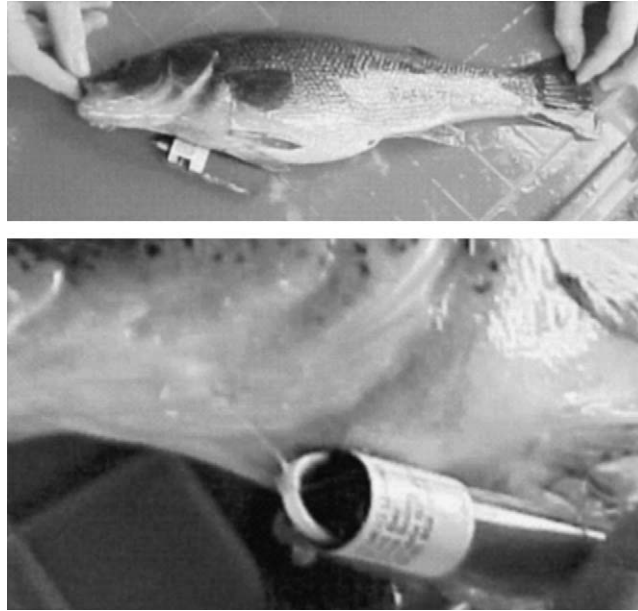


FIG. 2. Transmitter attached to *Percichthys trucha* at the junction of the preopercular and opercular bones and at the pelvic girdle.

on the transmitters, transported back to Lake Morenito and released in the shallow littoral zone of the lake (3 September 1999).

Before releasing the fish, eight VR1 receivers (VEMCO, 1998b) were activated and anchored with submersed buoys. The receivers were placed so as to obtain nearly complete coverage of Lake Morenito (Fig. 1), and seven receivers were retrieved 3 November 1999.

For the second trial, 10 healthy fish captured in Lakes West Morenito and Morenito in winter (August 2000) were transported to the hatchery, anaesthetized immediately, and the transmitters attached as above, but already switched on. The fish were released 2 days later (7 September 2000), from a boat, in a deep zone of West Morenito. Five VR1 receivers were anchored in the Lake Morenito system (Fig. 1), and were retrieved 15 November 2000.

Ultrasonic transmitters can be inserted into the fish body or externally attached. External attachment has the advantage of being less invasive, and has been used successfully in a variety of species (Carr & Chaney, 1977; Holland *et al.*, 1985; Marsac & Cayré, 1998), including *Morone americana* Gmelin 1789 (Mellas & Haynes, 1985) and *Sebastes* sp. L. 1758 (Matthews *et al.*, 1990). The anterior-ventral position used was employed by Claireaux & Lefrançois (1998) with *Dicentrarchus labrax* (L., 1758) and *Gadus morhua* L., 1758. One fish in the first trial with *P. trucha* descended over a period of weeks to the bottom and did not return to the surface, as did another in the second trial. All other fish showed 'normal' behaviour, spending part of the time in the shallow littoral areas and part of the time at greater depths, moving throughout the lake. The high level of survivorship as well as lack of erratic behaviour suggests that the tagging method was appropriate for monitoring behaviour of *P. trucha*.

DATA EXTRACTION AND ANALYSIS

The transmitters worn by the fish emit pings at a rate of *c.* 2 min⁻¹. When a fish enters the range of a receiver, the receiver records the fish ID, the date and time and the depth of the fish. It then continues to record the time of each received ping until

the fish leaves the receiver range. Receivers were retrieved, and the data processed with VEMCO (1998*b*) software to construct a database for each fish, indicating receiver, arrival and departure date and time, arrival depth, and number of pings recorded during its stay.

The database was then used to extract the following information: (1) depth time series (estimated from arrival depths), (2) number of hours (*e.g.* per day and per week) that a fish was recorded by a particular receiver and (3) approximate location of the fish. The radius of reception is *c.* 300 m, but can vary with temperature and wind, and the signal may be partially attenuated by the thermocline (Stasko & Pincock, 1977), and by dense vegetation or physical obstacles (Diana *et al.*, 1977; Matthews *et al.*, 1990). The range reached in a marine rocky reef habitat was estimated to be from 50 m to 1 km (Matthews *et al.*, 1990). Reception radius thus varied temporally, and the degree of overlap among receivers also varied over time. One consequence was that it was difficult to consistently determine fish location with accuracy. A second consequence was that a fish could appear to 'arrive' at a receptor without having moved. The time series of depth recordings appeared to be reliable; there were usually one to several recordings per hour, and recordings over short time periods were consistent. Interpreting spatial movements within Lake Morenito was more difficult due to many periods of simultaneous recording by several receivers. Movement into the channel area was most easily distinguished, as the channel receiver was placed far enough away that there was little overlap with other receivers. Other approximate locations could also be determined at times when nearly or completely continuous recording was observed for one receiver, while recordings by other receivers were more intermittent.

In the first trial (Lake Morenito), after a period of activity (ranging from 3 to 6 weeks), several fish suddenly became inactive, apparently remaining at constant depth and location. Explanations include the loss of the transmitters, the fish may have died, or the fish may have been resting or feeding within a limited area. This period of inactivity almost always followed a period of intense activity in the littoral zone. Because the cause of the marked change in behaviour was not known, 'inactive' fish were excluded from subsequent analyses.

In Lake Morenito, temporal patterns in (a) use of different depths, (b) use of the channel linking Lake Morenito to the larger lakes and (c) daily behaviour were examined for active fish. Although depth was recorded only upon arrival of a fish within the range of a receiver, fish typically moved in and out of the range of various receivers numerous times per day. This allowed the use of arrival depths to plot detailed patterns of depth use over time. To look at patterns of depth use over the entire study period, the depths recorded for each active fish were averaged over each 2 day interval, beginning on 4 September. Temporal patterns in use of different areas of the lake were determined by plotting the proportion of time that fish were recorded by receivers placed in the channel area (receiver 1), and the central part of the lake (receivers 4, 5 and 6). Time spent in each zone was summed over 2 day intervals, from 4 September, until the end of the study or until the fish became inactive. Daily patterns of activity were examined in two ways. First, the depth of each fish was determined, on an hourly basis, over the time period 14 September and 28 September. Nine of the 10 fish were clearly active throughout the period, and the 2 weeks included the full moon, and the previous 10 days. Second, the proportion of fish that were in the channel area was calculated, again on an hourly basis, and for the same 2 week period. Frequently after a fish entered the channel was recorded by the receiver, it 'disappeared' for hours, with occasional pings recorded by the channel receiver, and later it re-entered fully into the channel receiver range before returning to the main lake. It is suspected that these fish were in the part of the channel just outside the range of the receiver, and thus these 'disappearances' were counted as part of the channel visit in the analysis of daily behaviour.

In Lakes West and East Moreno, for each fish, (a) the pattern of depth use over time and (b) use of the different lakes were determined. As the receivers were placed farther apart, fish disappeared for much longer periods of time. They had to pass a receiver, however, to move into Lake Morenito or between West and East Moreno, and so movement among lakes could be reliably detected.

RESULTS

Most of the reproductive activity for *P. trucha* occurs in the spring and summer, with peak proportions of gravid females and ripe males observed in November to December [Fig. 3(a), (b)]. Lake Morenito is shallow and warms up faster in the spring than the larger Lakes Moreno East and West, with spring water temperatures (November) 2–3° C warmer in Lake Morenito, and summer temperatures up to 5° C warmer [Fig. 3(c)]. The winter and spring of 2000 were cooler than those of 1999; in November, water temperature was 2.5° C lower [inset, Fig. 3(c)]. As a result, reproduction began earlier in 1999 than in 2000; of the individuals caught in West Moreno in early September of 1999, 18% of the males were ripe, and 28% of the females were gravid [Fig. 3(b)]. No fish were reproductive at this time in 2000.

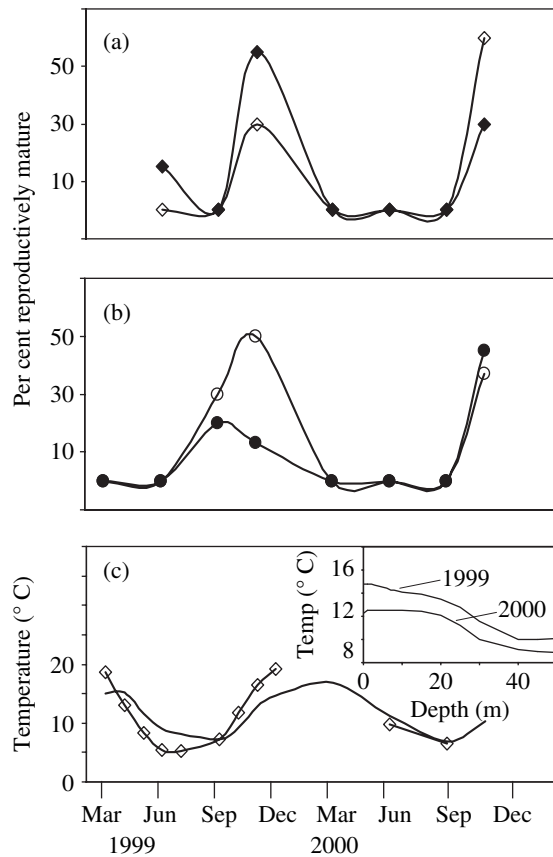


FIG. 3. Reproductive status of the population and water temperature. Proportion of vitellogenic females (◆, ●) and males (◇, ○) that were ripe in captures from (a) Lake Morenito and (b) Lake West Moreno. (c) Temporal change in surface water temperature for Lakes Morenito (line and ◇) and West Moreno (line). Inset contains spring (November) temperature depth profiles for Lake West Moreno in 1999 and 2000.

BEHAVIOUR DURING SPAWNING PERIOD: LAKE MORENITO (1999)

All fish appeared to move throughout Lake Morenito; all were recorded by all receivers (with the exception of the channel receiver) at some point during the 2 months. Eight of the 10 fish visited the shallow pondweed channel at some point during the study, and the pattern of channel use appeared to be linked to the lunar cycle [Fig. 4(a)]. Time spent in the channel area peaked near the time of the full moon, corresponding to a decrease in time spent at the centre of the lake. Use of the channel area declined again a few days after the full moon. Of the five fish that used the channel area most extensively, four were known to be ripe males. The temporal change in spatial behaviour coincided with a change in average depth [Fig. 4(b)]. Over the first 2 weeks of September,

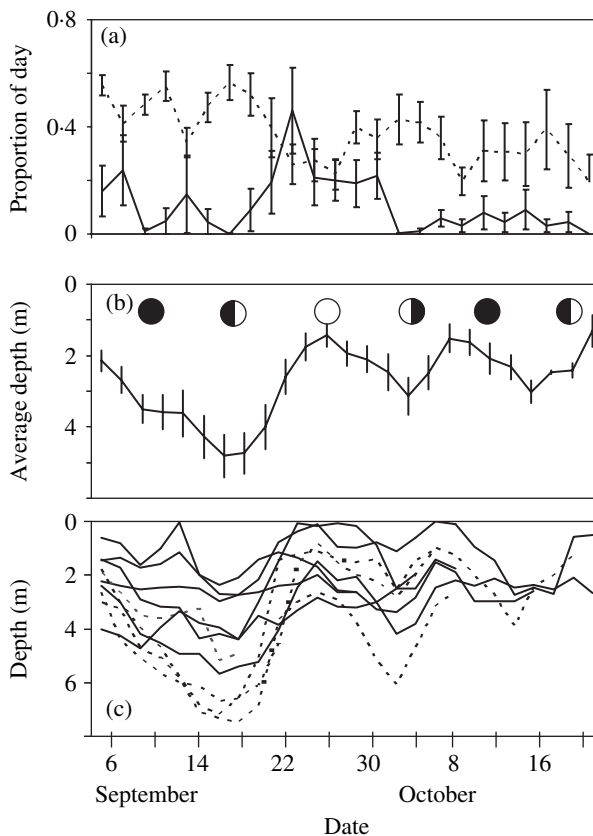


FIG. 4. Spatial and depth activity profiles for *Percichthys trucha* during the spawning season (1999). (a) Mean \pm s.e. proportion of time (per 48 h period) spent by active fish in the vegetated channel area (—) connecting Lake Morenito to the larger lakes, and in the central zone of Lake Morenito (---) over the course of the study. (b) Mean \pm s.e. depth and moon phases (full moon in white), and (c) individual depths (per 48 h period) calculated for active fish, ripe males (—) and unknown sex fish (---), over the study period.

the fish slowly descended, from an average depth of 2 m to an average of 5 m. Descent was slow, individual fish always spent one to several days at a particular depth before moving deeper. There was considerable variation in the behaviour of individual fish, and in particular, individuals identified as ripe males showed a lower tendency to descend during this period [Fig. 4(c)]. A few days prior to the full moon, there was a relatively quick ascent, to an average depth of just over 1 m [Fig. 4(b)]. All active fish were in relatively shallow water at this time. After a few days to a week near the surface, fish tended to descend again. Another period of surface activity occurred just before the new moon. Between 1 and 22 October, six of the fish dropped rapidly (over a period of hours) to a particular depth, and then remained at that depth and in or near that location for the remainder of the study period. In each case, the rapid descent occurred immediately after a period of surface activity.

Daily behaviour was most pronounced during the period of surface activity encompassing the full moon (Fig. 5). During this period, nights were typically spent in or near the littoral zone (≤ 2 m depth) and days were spent in slightly deeper water. Fish tended to move to shallower waters at dusk (1800–2000 hours) and return to deeper water by dawn (c. 0600 hours) [Fig. 5(a)]. The depth changes associated with this behaviour were relatively small (1–2 m). For some of the fish, the daily depth shifts were also associated with relatively large spatial movements, from the main part of Lake Morenito, to the channel area [Fig. 5(b)]. A few fish stayed in the channel area throughout the day and night, particularly on days close to the full moon, but others visited the channel at dusk, returning to the main lake at, or just prior to dawn. Nights were also spent in the littoral zones at the extreme western side of the lake, and, one fish visited the littoral zone on the eastern side, disappearing for

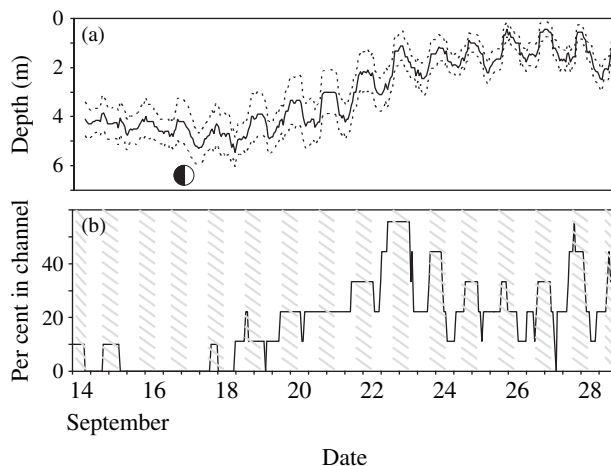


FIG. 5. Daily behaviour of *Percichthys trucha* during the spawning period (1999). (a) Mean (—) and s.e. (···) depth calculated for active fish, and (b) proportion of fish using the channel area over the 2 week period leading up to, and encompassing the full moon (in white) (▨, nights). Depths and proportions were calculated on an hourly basis.

periods of time, probably to Ezquerra Pond. Though a few fish exhibited some daily behaviour during the first weeks of the study, there was no overall daily pattern of depth use prior to about 20 September [Fig. 5(a)] and the fish that were slowly descending showed no evidence of spatial or depth shifts at dusk or dawn.

BEHAVIOUR DURING PRESPAWNING PERIOD: LAKE MORENO (2000)

There was a great deal of variation among the fish in pattern of movement in the larger lake system (Fig. 6). The range of depths used by obviously active fish was 0–10 m, but most fish spent nearly all of the time between depths of 0 and 5 m. As the receptors did not cover the entire lake system, all fish disappeared for periods of time.

The largest four fish went immediately to Lake Morenito (Fig. 6). Three fish (VI, VII and VIII) stayed in Morenito, and displayed a pattern similar to fish the previous year, slowly descending to depths of 5–6 m, and then returning to the surface. The fourth fish (III) spent almost 2 weeks in the littoral zone, then disappeared within Morenito for another 2 weeks, and finally returned to Lake Moreno. Two additional fish also went to Morenito, after spending weeks in the larger lake system. While in Lake Moreno, both fish slowly descended over the first weeks, fish IV to 5 m, and fish X to 10 m. Fish IV visited Morenito briefly a few days after the study began, but returned to West Moreno for an additional 2 weeks, before re-entering and staying in Morenito. Fish X went to the eastern part of East Moreno, and apparently spent the entire time in this lake until 1 week before the end of the study, when it, too, went to Morenito. It covered the distance from the receiver at the east end of the lake to the receiver at entrance to Morenito (4 km) in *c.* 2 h.

The four smallest fish did not use Lake Morenito during this study. Three fish (I, II and V) apparently stayed in West Moreno and were recorded from both receivers in that lake. Fish I and II disappeared partway through the study, while fish V disappeared for periods of time, but always reappeared in roughly the same area. One fish (IX) either lost its transmitter or died; it descended immediately to 21 m and remained in the range of the two receptors in West Moreno.

DISCUSSION

In this study, 20 *P. trucha* were tracked for up to 2 months, 10 individuals during the spawning season of 1 year, and 10 individuals in the following year, beginning before the fish had mature gonads. Movement of individual fish among the interconnected lakes in the Lake Moreno system was documented during the prespawning season, as was movement from the larger lakes into the smaller, shallow Lake Morenito. In contrast, fish observed during the breeding season in 1999 stayed in Lake Morenito for the duration of the study. Changes in behaviour during the breeding season appeared to be linked to the lunar cycle, with an increased tendency to move into the shallow littoral zones at dusk, in the days leading up to, and immediately after, the full moon.

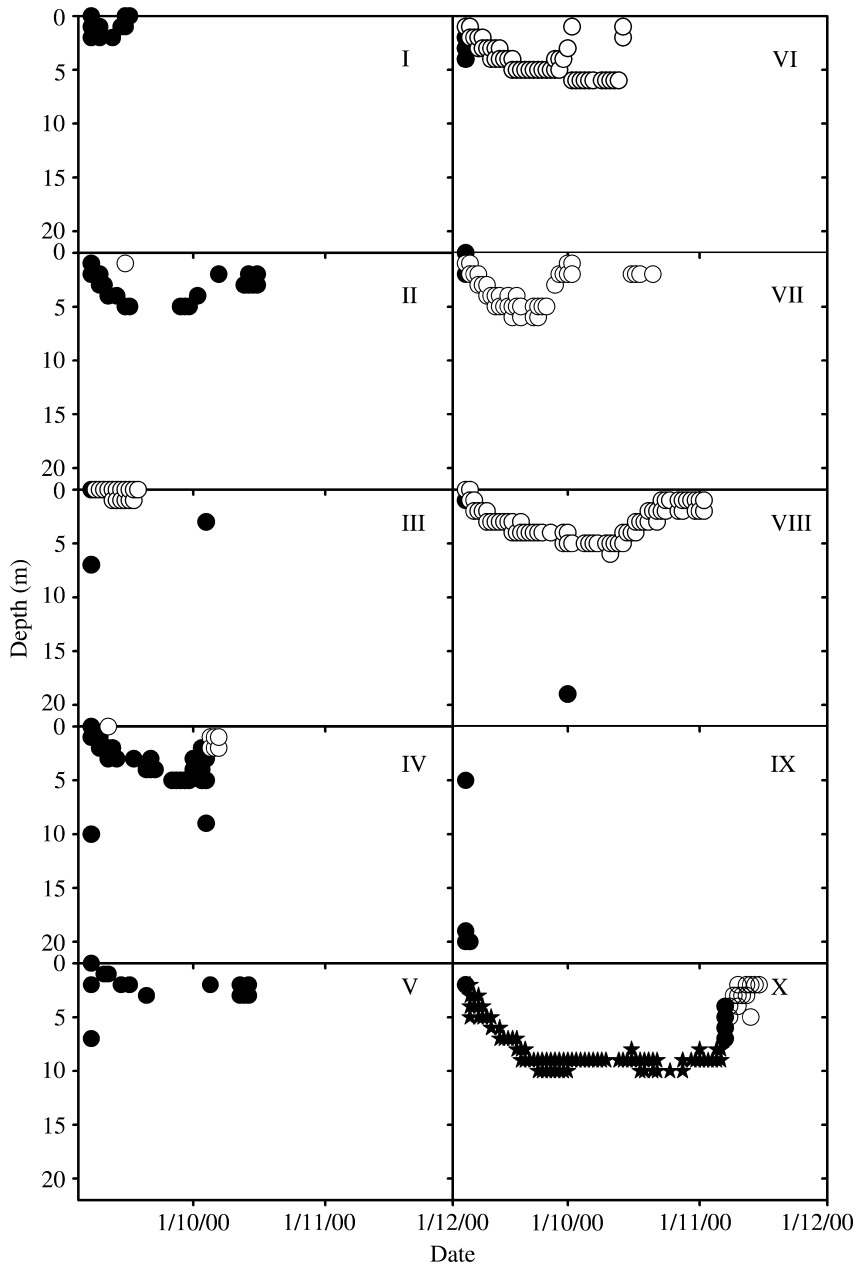


FIG. 6. Temporal pattern of distribution and depth use by individual *Percichthys trucha* (I–X) during the prespawning season in the lakes East Moreno (★), West Moreno (●), and Morenito (○) in 2000.

Attachment of transmitters has the potential to alter fish behaviour, due to added energy costs or by interfering with swimming and feeding (Diana *et al.*, 1990), and it is therefore possible for the observed behaviour to be abnormal. Various limits for the ratio of transmitter mass to fish mass have been

suggested, 4.2% (Claireaux & Lefrançois, 1998), 3% (Winter, 1983; Summerfelt & Mosier, 1984), 14.5% (Moser *et al.*, 1990) and 5% (McCleave & Stred, 1975; Diana *et al.*, 1990). The highest ratio in this study (3.2%) is toward the lower end of this range, and fish with transmitters attached swam normally in captivity. Thus, the transmitter mass probably had minor effects, at least early in the studies, though it is possible that there was a more significant cumulative energetic cost toward the end of the observations. External attachment was chosen because it is quick and non-invasive, and thus less likely to cause mortality, and because others using the method reported normal behaviour (Matthews *et al.*, 1990; Claireaux & Lefrançois, 1998; Herke & Moring, 1999). Two fish showed aberrant behaviour in the early weeks of the study, descending to depths and remaining there, apparently immobile. In the first year, the descent was slow and by the smallest fish; it is likely that it died and possible that carrying an extra 3% mass contributed to its death. The fish that apparently dropped immediately to 21 m in the second year, however, was not the smallest, and both the timing and speed of the descent suggests that it lost its transmitter. The similarity of the behaviour of the remaining fish of different sizes (including between years) suggests that the transmitters were not causing abnormal behaviour.

This study provides the first data on the range or type of movement characteristic of *P. trucha* in Patagonian lakes. It has demonstrated that individual *P. trucha* are capable of moving, and do move, throughout the entire Lake Moreno system. Most of the individuals tracked in the larger lakes, however, were recorded from much more restricted regions within the lake system, prior to moving to the small, shallow Lake Morenito. Restricted movement is typical of many fishes (Cole & Moring, 1997; Danancher *et al.*, 2004; Grant & Keely, 2004), including an Australian percichthyid [*Macquaria ambigua* (Richardson, 1845)], which exhibits short distance movements within a home range for most of the year, though the location of the home range may shift over time (Crook, 2004; O'Connor *et al.*, 2005). The North American *Morone saxatilis* (Walbaum, 1792) shows similar movement patterns (Jackson & Hightower, 2001). More work on the behaviour of *P. trucha* in the non-spawning period is needed to determine the extent to which its movement is restricted during the non-breeding season.

This study supported the hypothesis that fish move from the larger Lakes Moreno East and West into Lake Morenito in early spring. The shallow, warm Lake Morenito appears to be a key breeding ground for the *P. trucha* population in the Lake Moreno system. It has an extensive vegetated littoral zone suitable for spawning, and egg masses have been found on littoral collectors placed among aquatic plants at depths of 1–3 m (M. Battini, pers. obs.). In addition, warmer temperatures in spring and summer may promote faster maturation of gonads. Longer-distance movements associated with spawning are not uncommon in freshwater fishes (Rodríguez-Ruiz & Granado-Lorencio, 1992; Sandlund *et al.*, 1992), and have been reported for Australian Percichthyidae (Cadawallader & Rogan, 1977; Simpson & Mapleston, 2002; O'Connor *et al.*, 2005). Use of small, warm lakes for prespawning and spawning activity has also been documented for *Morone chrysops* (Rafinesque, 1820) (Beck & Willis, 2000). *Percichthys trucha* has an extended period of reproduction in these lakes, and this was reflected in the wide variation in the date on which fish entered

Morenito. Larger fish may be ready to breed earlier, as suggested by the fact that the four fish to enter Morenito immediately (early September) were the largest of the 10, and the four had not entered by early November were the smallest individuals. The mixing of individuals from throughout the lake system during the reproductive period suggests that the *P. trucha* in the Lake Moreno system probably comprised of a single population.

Little is known about the behaviour of *P. trucha* during its reproductive period. As is common for fishes in temperate lakes (Thorpe, 1977; Wootton, 1991), *P. trucha* in Andean lakes appear to have a single annual breeding period in late spring and summer (though reproductive individuals have occasionally been found in winter samples). Gonad maturation is probably temperature-dependent, and a 2° C difference in spring water temperature was associated with a later onset of reproduction in 2000 (Fig. 3). The breeding season had already begun when the Morenito study was initiated in September 1999, as indicated by the presence of females with fully developed eggs, and the fact that half the tagged fish were ripe males, and thus the behaviour observed during this period is interpreted as behaviour characteristic of the spawning period.

A variety of environmental factors have been implicated as spawning cues for freshwater fishes, including water temperature, lunar cycle and photoperiod (Stancey, 1983; Cussac & Maggese, 1987; Rodríguez-Ruiz & Granado-Lorencio, 1992; Groenenberg & Cussac, 1993; Watanabe, 2000). This study found an association between the lunar cycle and behaviour probably related to spawning. Fish were released in the littoral zone of Lake Morenito just before the new moon. Five of the fish spent the first 10 days slowly descending, moving toward the central part of the lake. During this phase, there was no strong daily movement pattern; rather, fish remained at a particular depth day and night, over several days, before moving deeper. Similar patterns of descent were seen the following year, for three of the fish that entered Morenito early, as well as for two fish that remained in Moreno for a time. A descent over a period of weeks has also been reported for *Coregonus clupeaformis* (Mitchill, 1818) (Bégout Anras *et al.*, 1999). This is probably an energetically efficient manner of feeding, as these fish must adjust gasbladder volume by active secretion from and re-absorption to the blood (Randall *et al.*, 1997). As there were no movements to the littoral zone by these fish during this time, it is assumed that the fish were feeding.

The return to shallower water (vegetated littoral zone) was relatively synchronized and coincided with the full lunar phase. It was also rapid compared with the descent, occurring over a 1–2 day period for individual fish. Change in depth was linked to spatial changes. Nine fish, including those that had remained in shallower water went to identifiable littoral locations at this time (one fish had become inactive before this period). Six of the nine fish visited the shallow pondweed channel that connects Morenito to the larger lakes at this time, and the other three went to the littoral zones in the extreme west or extreme east of the lake. These areas, particularly the channel area appear to be key spawning locations within the lake. Reproductive behaviour has not been observed for *P. trucha*, but spawning in the related *M. americana* and *M. chrysops* involves co-ordinated and ritualized movements by several fishes, usually with one female attended by, and in close contact with several

to many males. For species with group spawning behaviour, the lunar cycle may serve as a cue for aggregating in specific spawning locations. Response to the lunar cycle is commonly seen in marine species (Garcia, 1992; Findlay & Allen, 2002), and spawning at full moon has also been reported for freshwater fishes (Bégout Anras *et al.*, 1999).

Co-ordinated daily behaviour patterns were most evident during the period leading up to, and encompassing the full moon, the period when all fish were active in and near the littoral zone. Daily behaviour has been documented for many types of fishes (Naud & Magnan, 1987; Guy *et al.*, 1992; Perrow *et al.*, 1996; Clough & Ladle, 1997; Crook, 2001). In this study, individual *P. trucha* moved into shallower water (nearer shore) at dusk (1800–2000 hours), and returned offshore, often at dawn (*c.* 0700 hours) but sometimes several hours earlier. Thus, daylight hours were spent deeper and nearer the centre of the lake, a pattern suggested to be associated with feeding and predator avoidance in some Australian Percichthyidae (Crook, 2001; Simpson & Mapleston, 2002). Most of the movements at dusk during this period were to the channel linking Morenito to the larger lakes or toward the western area covered by receiver 3, just north of the channel (Fig. 1). These areas are shallow and filled with vegetation and correspond to where egg masses have been seen (M. Battini, pers. obs.). A few of the movements were to the east, past the more easterly receptor, and probably to the shallow and vegetated Pond Ezquerria. The larger fish known to be ripe males spent many nights visiting these areas, particularly the channel site. Thus the behavioural data suggest that spawning takes place mostly at night, that the channel is a key spawning location for *P. trucha* in the Lake Moreno system, and that areas to the extreme east and west are also used, but to a lesser extent. While *M. chrysops* show similar daily inshore and offshore movements during the spring, moving inshore to spawn, their spawning and inshore activity occur in the day (Beck & Willis, 2000).

Shortly after a period of intense surface activity (spawning), six fish descended to a particular depth and showed little movement, remaining within a restricted area in Lake Morenito for the duration of the study. It is possible that these fish had died. Several factors, however, suggest that this may have been a postspawning 'resting' phase, as has been observed for *Leuciscus Leuciscus* (L., 1758) (Clough *et al.*, 1998). The sudden descent was quite synchronized for four of the fish, occurring at the new moon, immediately following surface activity. Second, arrivals and departures were recorded by receivers during the period of inactivity, and no fish was continuously recorded by a single receiver throughout the period. Third, two of the fish, after being recorded at a constant depth for a period of time, began to be received at two different depths. Without retrieval of the fish, however, it was not possible to determine if they were alive and resting, or dead.

This study has shown long distance movement within a lake system of more than 10 km², and demonstrated that individuals move from the larger lakes to a small, shallow warmer lake in the prespawning period, suggesting that the *P. trucha* with the Lake Moreno system probably belong to one reproductive unit. These results are of importance in setting conservation criteria for this endemic species, and have implications for construction and the development of tourism in this and similar lake systems in mountain areas of Patagonia (*e.g.* severing

the connection to Lake Morenito might be damaging for the population). More work needs to be done to assess the frequency of long distance movements, and to determine whether they are primarily associated with movement to spawning areas. There was considerable variation in date of entry to Morenito; larger fish entered earlier, but other factors such as sex and condition could well be important.

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