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Abstract

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Keywords

Iowa, common carp, nuisance species, sport fishery, aggregation, habitat selection

Disciplines

Aquaculture and Fisheries | Environmental Monitoring | Natural Resources and Conservation | Natural Resources Management and Policy

Comments

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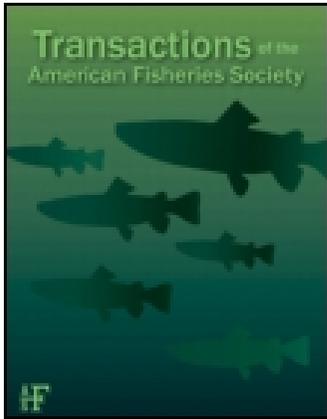
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Seasonal Distribution, Aggregation, and Habitat Selection of Common Carp in Clear Lake, Iowa

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Abstract.—The common carp *Cyprinus carpio* is widely distributed and frequently considered a nuisance species outside its native range. Common carp are abundant in Clear Lake, Iowa, where their presence is both a symptom of degradation and an impediment to improving water quality and the sport fishery. We used radiotelemetry to quantify seasonal distribution, aggregation, and habitat selection of adult and subadult common carp in Clear Lake during 2005–2006 in an effort to guide future control strategies. Over a 22-month period, we recorded 1,951 locations of 54 adults and 60 subadults implanted with radio transmitters. Adults demonstrated a clear tendency to aggregate in an offshore area during the late fall and winter and in shallow, vegetated areas before and during spring spawning. Late-fall and winter aggregations were estimated to include a larger percentage of the tracked adults than spring aggregations. Subadults aggregated in shallow, vegetated areas during the spring and early summer. Our study, when considered in combination with previous research, suggests repeatable patterns of distribution, aggregation, and habitat selection that should facilitate common carp reduction programs in Clear Lake and similar systems.

The common carp *Cyprinus carpio* is an adaptable freshwater species that is capable of rapidly colonizing pristine as well as disturbed habitats (Panek 1987; Koehn 2004). The species is globally distributed and has firmly established populations on every continent except Antarctica (McCrimmon 1968; Lever 1996). Common carp are native to eastern Europe and Asia, where they are important sport and food fish. However, in North America and Australia, common carp are highly invasive; they overpopulate many systems and degrade water quality, often contributing to declines in native fishes (Bernstein and Olson 2001; Koehn 2004). On these two continents, overabundant common carp populations have prompted millions of dollars in research and control efforts (Roberts and Tilzey 1997; Pimentel et al. 2000). Although commercial fishers, sport fishers, fisheries biologists, and the general public differ in their views regarding the value of common carp, most would acknowledge the dominant role the species plays in the systems it inhabits (Lubinski et al. 1986).

Despite the widespread abundance and notoriety of common carp, their ecology has received relatively little study in natural systems (Crivelli 1981; García-Berthou 2001). Numerous studies conducted in culture

ponds, enclosures, and mesocosms have documented the detrimental effects of this species on water quality, macrophytes, and invertebrate fauna (Rose and Moen 1952; Crivelli 1983; Breukelaar et al. 1994; Roberts et al. 1995; Parkos et al. 2003; Miller and Crowl 2006); however, information on common carp distribution patterns and habitat use is sparse. Previous research on common carp movement has shown them to exhibit both site fidelity and high mobility (Reynolds 1983; Crook 2004; Stuart and Jones 2006). In southeast Australia, common carp have been observed to establish restricted home ranges but also to move over 200 km (Crook 2004; Stuart and Jones 2006). Some individuals in river systems have been documented as moving at a rate of 8 km/d (Stuart and Jones 2006), which indicates that populations are capable of rapidly changing their spatial distribution. Seasonal variation in the distribution of adult common carp has been reported and is thought to be primarily driven by habitat, lake morphometry, spawning, and seasonal factors; the collective evidence suggests that common carp aggregate in shallow, vegetated areas during spring spawning, scatter in littoral habitats during summer, and move to relatively deeper water to overwinter (Swee and McCrimmon 1966; Johnsen and Hasler 1977; Otis and Weber 1982; Horvath 1985; García-Berthou 2001).

Clear Lake is a valuable natural resource for Iowa (Downing et al. 2001). It is the state's third-largest

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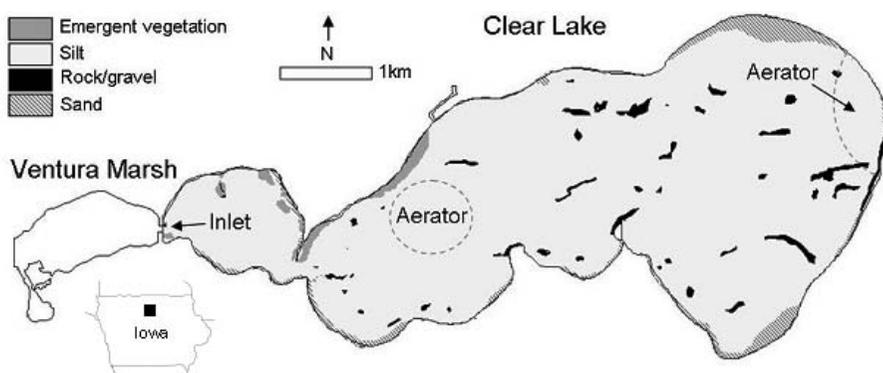


FIGURE 1.—Map of vegetated areas, substrates, and landmarks in Clear Lake, Iowa, where common carp distribution, aggregation, and habitat selection were studied. The aerators operate when the lake is ice covered. Inset at lower left shows the lake's location within the state.

natural lake and is a popular recreational site (Azevedo et al. 2001; Wahl 2001). For a variety of reasons, water quality in Clear Lake has been steadily degrading since the 1940s; nutrient levels have increased, algal concentrations and nuisance blooms have increased, lake depth has decreased, water clarity has declined, and formerly abundant aquatic vegetation has virtually disappeared in many areas (Downing et al. 2001). Coupled with these changes in water quality are major changes in the fish community. Due to loss of habitat, native centrarchids (bluegill *Lepomis macrochirus*, crappies *Pomoxis* spp., and largemouth bass *Micropterus salmoides*) that rely on aquatic vegetation for spawning and cover have declined and are being replaced by a burgeoning community of benthic rough fish (including common carp) that are tolerant of degraded water quality conditions (Wahl 2001).

The common carp is both symptomatic of the decline in overall environmental health of Clear Lake and a potential roadblock to improvement (Wahl 2001; Schrage and Downing 2004). Common carp activity resuspends large amounts of sediment into the water column, which in combination with physical uprooting of macrophytes and consumption of benthic invertebrates results in reduced water clarity, habitat, and food for other fish species (Bonneau 1999; Schrage and Downing 2004). High common carp biomass also results in high internal loading of dissolved nutrients through excretion, effectively transferring nutrients from the sediments back into the water column (Lamarra 1975; Chumchal et al. 2005). Common carp essentially constitute a positive feedback mechanism, whereby the biomass and deleterious influence of these fish increase as water quality continues to deteriorate. The natural mechanism of predatory control by piscivorous fish species is also lost as their abundance

declines with decreases in water quality (Bonneau 1999). Understanding common carp seasonal distribution, aggregation, and habitat selection is the first step towards a long-term control strategy for this species in Clear Lake and should also help guide similar common carp control programs elsewhere.

The goal of our study was to explore patterns of distribution and dispersion by common carp in Clear Lake for the purpose of guiding future control strategies. Our specific objectives were to use radiotelemetry to characterize the seasonal distribution, aggregation, and habitat selection of adult and subadult common carp.

Study Area

Clear Lake is a eutrophic, glacial lake located in north-central Iowa (43°08'N, 93°22'W; Figure 1). It has a surface area of 1,468 ha, shoreline development index of 1.6, maximum depth of 5.9 m, mean depth of 2.9 m, and summer Secchi disk transparency of 0.3–0.4 m (Downing et al. 2001). Clear Lake is polymictic, and stratification is rare due to near-continuous mixing by wind and wave action (Downing et al. 2001). Lake temperature in 2005 ranged from less than 4.0°C in winter to 28.5°C in July. The majority of the lake bottom is composed of silt flats, and a few scattered rocky reefs and sandy areas are also present (Downing et al. 2001; Figure 1). Macrophytes occupy approximately 1% of the lake surface area (Egertson et al. 2004). Giant bulrushes *Scirpus validus* and cattails *Typha* spp. dominate the macrophyte community and are particularly abundant along the northern shoreline. To the west lies Ventura Marsh, a shallow, 81-ha wetland. Flow from Ventura Marsh enters Clear Lake at a narrow inlet that contains a barred iron gate to prevent fish passage (Figure 1).

Methods

Telemetry.—Common carp were collected for telemetry by boat electrofishing the perimeter of Clear Lake and Ventura Marsh each October and April from 2004 to 2006. Captured fish were weighed (nearest g) and measured (nearest mm total length [TL]), surgically implanted with radio transmitters, and returned to the lake. Fish were separated into adult (483–790 mm TL; 1,542–7,530 g) and subadult (203–330 mm TL; 150–490 g) life stages. Gonads from a sample of fish classified as subadults were examined for the presence of mature oocytes to ensure that the fish had not reached sexual maturity. Fish were implanted with one of two sizes of transmitter to minimize the ratio of transmitter weight : body weight. All transmitters were manufactured by Advanced Telemetry Systems (Isanti, Minnesota). Transmitters for adult fish (Model F1235) weighed 25.0 g in air and had a life expectancy of 25 months. Transmitters for subadult fish (Model F1030) weighed 2.1 g and had a life expectancy of 83 d.

Electroanesthesia (170–240 V) was applied to fish before surgery to induce muscle relaxation (Summerfelt and Smith 1990). Once anesthetized, fish were placed ventral side up in a V-shaped foam cradle that was positioned partially in water to allow immersion of the gills and normal ventilation. A short line of scales was then removed from just off center and to the left of the ventral midline, beginning at the posterior margin of the left pelvic fin and ending just before the anus. An incision (3 cm in adults; 1 cm in subadults) was then made in the center of the scaleless region. The transmitter was inserted into the body cavity and pushed just ahead of the incision. Subsequently, a large needle containing the transmitter's external whip antenna was used to create a small hole in an area of the body wall located posterior and lateral to the incision, allowing the external antenna to be threaded to the fish's exterior (Ross and Kleiner 1982). The incision was closed, the two incision planes were aligned, and two to four interrupted surgeon's knots were tied using external suture material (3–0, monofilament, nonabsorbable). After surgery, the incision was cleansed with saline solution and the fish was put in a holding tank to recover. Surgical tools were sterilized before each surgery using a solution of water and Nolvasan disinfectant (chlorhexidine diacetate).

Adult fish were implanted with radio transmitters in October 2004 ($N = 30$). Additional groups of adults received transmitters in October 2005 ($N = 21$) and April 2006 ($N = 3$) to replace fish that had lost transmitters or died. An initial group ($N = 15$) of subadults was implanted with transmitters in April 2005, and a second group ($N = 45$) received transmitters in April 2006 to

replace the initial sample for which transmitter batteries had expired. Subadult sample size was increased in 2006 to offset transmitter loss, which was expected to be considerable based on the number of losses in the 2005 sample.

Tracking of adult fish was conducted year-round over 22 months (November 2004–August 2006). Because of the relatively short life of the smaller transmitters, subadults were tracked from the time of transmitter implantation in April until transmitters expired in July and August. During the open-water season (March–November), tracking was done by boat and took place an average of nine times per month. When sufficient ice was present (January–March), tracking was done by all-terrain vehicle and was conducted seven times per month on average. No tracking was conducted during December due to hazardous conditions for boat launching, boating, and working on thin ice. To ensure equal sampling of all areas of the lake, a series of 27 parallel transects was established on a map of Clear Lake and programmed into a Global Positioning System (GPS) receiver. We systematically searched along these transects during each tracking session. The starting location of a tracking session was randomly assigned by rolling a six-sided die with each number corresponding to a different starting point. Water temperature was recorded at the beginning and end of each tracking session. When a fish was located, Universal Transverse Mercator coordinates and depth at the location were recorded.

The approach to locating fish varied by season, ice conditions, and depth occupied by the fish. Fish detected in deeper water (≥ 1.5 m) or under ice were approached directly and were assumed to be directly below when signal strength was equal in all directions (Guy et al. 1994). For detections in shallow water (< 1.5 m), there was a concern that hovering directly over fish could alter their behavior (Winter 1996); therefore, we maintained a distance of approximately 10 m and estimated location based on signal strength. We used triangulation to estimate the location of fish when ice conditions were deemed unsafe. Blind tests with transmitters placed in the lake were used to assess the accuracy of each location technique. Locating fish from directly above in open water was accurate to within 6 m, while using the same technique on ice was accurate to within 3 m. Estimating the location of fish in shallow water was accurate to within 10 m.

Fish that were located within 5 m of their previous location over three consecutive tracking sessions were investigated for transmitter loss or mortality. In depths of 2 m or less, we used an underwater probe described by Fellers and Kleeman (2003) to recover transmitters

with a success rate of 100%. In depths greater than 2 m, transmitter loss or death was concluded after 10 consecutive locations were made in the same area. Data from fish that were judged to have perished or experienced transmitter loss within a month of surgery were omitted from the data set.

Analysis of seasonal distribution and aggregation.—Adult and subadult common carp distribution was examined at monthly and seasonal scales. Seasons were defined as December–February (winter), March–May (spring), June–August (summer), and September–November (autumn). For each month and season, the mean water temperature, mean depth, and mean distance to shore for all fish locations were calculated. For each season, differences among means for each variable (temperature, depth, distance to shore) were tested with repeated-measures analysis of variance (ANOVA) using the MIXED procedure in the Statistical Analysis System version 9.1 (SAS Institute 2004).

Maps of adult and subadult monthly distribution and aggregation were created using kernel estimators and geographical information systems (GIS) software. For each complete tracking session, the coordinates of all fish locations were plotted and a fixed kernel utilization distribution (UD) with a 50% probability contour was computed using the Animal Movement Analyst Extension (Hooge and Eichenlaub 1999) in ArcView version 3.3. Kernel analysis creates contour lines around areas of concentrated use. The 50% probability contour, which encompassed the smallest area containing approximately one-half of the fish locations, was defined as the area of core activity (Hooge et al. 2001) and was considered to be an index of the level of population aggregation during each complete tracking session. Aggregations of fish were indicated by small core activity areas. Temporal trends of aggregation were assessed by calculating and comparing the mean core activity area for each month. Aggregation areas were then identified visually by inspection of monthly common carp distribution maps.

Monthly distribution maps were constructed from a series of modified kernel UD shapefiles. Each kernel UD was composed of a 95% probability contour and up to four additional contours, depending upon the level of aggregation exhibited. A set of criteria based on maximum core activity area was used to award additional contours at the 70, 50, 30, and 10% probability levels. Utilization distributions in which fish were more aggregated received more probability contours, allowing areas of concentrated use to be readily identified. Each monthly distribution map was then created by combining all kernel UD for that particular month. When probability contours over-

lapped, areas with the same level of aggregation were merged, while areas of stronger aggregation were expressed over weaker ones. The end result of this process was a series of monthly maps in which greater aggregation was represented by more probability contours and areas of aggregation were identified by darker shading.

Analysis of habitat selection.—Common carp seasonal distribution was examined in relation to eight habitat types that were based on a combination of different lake substrates and depths. Substrates were classified as silt, sand, rock, and aquatic vegetation. Depths were classified as shallow (<2 m), middepth (2–4 m), and deep (>4 m). Silt and rock were found in all depths, while sand and aquatic vegetation were only found in shallow water. Habitat availability was quantified using a map of Clear Lake habitat created with GIS software. Habitat types were represented in the digitized Clear Lake map as follows: shallow, silty habitat (22.9%); shallow, rocky habitat (0.9%); shallow, sandy habitat (4.3%); shallow, vegetated habitat (1.5%); middepth, silty habitat (61.0%); middepth, rocky habitat (1.0%); deep, silty habitat (8.3%); and deep, rocky habitat (0.1%). Depth and silt, rock, and sand substrates were delineated using a digitized bathymetric lake map (Iowa Conservation Commission 1971; Iowa State University Limnology Laboratory 2005). Egertson et al. (2004) determined that less than 1% of Clear Lake's submerged macrophytes were located outside of emergent vegetation areas. Using this information, we delineated areas of aquatic vegetation by tracing the perimeter of emergent macrophyte beds on foot during ice cover with a handheld GPS unit. Position accuracy of the GPS unit was 3.0 m. The GPS log was projected into an existing GIS map and digitized to quantify available aquatic vegetation.

Habitat selection was assessed by comparing proportional habitat use in relation to availability. Habitat use by individual fish was defined as the percentage of locations within each habitat type. Chi-square tests with log-likelihood test statistics were used to evaluate whether fish were using habitats differently, thus demonstrating selection for specific habitats (Manly et al. 1993). Selection ratios (use : availability) with 95% confidence intervals were calculated and used to determine habitats that were positively selected by common carp (Thomas and Taylor 1990; Manly et al. 1993; Rogers and White 2007).

Results

Location Statistics

From 20 November 2004 to 9 August 2006, we recorded 1,951 locations, of which 1,600 were from

TABLE 1.—Seasonal and monthly mean ($\pm 95\%$ confidence interval) water depth at location sites (m) and distance to shore (m) recorded for radio-tagged adult common carp in Clear Lake, Iowa, 2005–2006. Mean lake temperature ($^{\circ}\text{C}$) for each season or month is also shown. Within a column, seasonal means followed by the same letter are not significantly different ($P > 0.05$).

Season or month	Mean temperature ($^{\circ}\text{C}$)	Mean depth (m)	Mean distance to shore (m)
Winter	0.1 ± 0.0 z	2.3 ± 0.1 z	402 ± 27 z
Jan	0.1 ± 0.0	3.2 ± 0.1	607 ± 49
Feb	0.1 ± 0.0	2.0 ± 0.2	317 ± 31
Spring	12.4 ± 0.4 y	1.7 ± 0.1 y	209 ± 25 y
Mar	1.7 ± 0.3	2.5 ± 0.3	335 ± 58
Apr	11.2 ± 0.4	1.9 ± 0.2	255 ± 36
May	15.7 ± 0.5	1.5 ± 0.2	155 ± 25
Summer	24.3 ± 0.1 x	1.6 ± 0.2 y	198 ± 36 y
Jun	23.0 ± 0.2	1.6 ± 0.2	175 ± 38
Jul	25.1 ± 0.3	2.0 ± 0.3	290 ± 74
Aug	25.0 ± 0.2	1.8 ± 0.3	245 ± 73
Autumn	9.3 ± 0.8 w	2.2 ± 0.3 z	335 ± 54 x
Sep	21.8 ± 0.3	2.1 ± 0.7	321 ± 133
Oct	11.6 ± 0.6	2.2 ± 0.4	322 ± 74
Nov	4.5 ± 0.5	2.2 ± 0.3	335 ± 57

adults and 351 were from subadults. The number of adult locations varied by season: 237 in winter, 514 in spring, 554 in summer, and 295 in autumn. Seven adults that received transmitters in 2004 and 13 that received transmitters in 2005 were still alive and had active transmitters at the end of the study period. The median number of locations for individual adults was 37; the minimum was 23 and the maximum was 88. Of the 60 subadults with transmitters, 36 remained alive until their transmitter batteries expired. The median number of locations for individual subadults was five; the minimum was 3 and the maximum was 25.

Seasonal Distribution and Aggregation

The mean depth of areas where adult common carp were located ranged from 1.5 to 3.2 m, which encompasses 29% of the lake’s available depth (Table 1). The deepest sites of adult locations were recorded in January (3.2 m), when the lake surface was frozen, but adults were rarely found in water deeper than 4.0 m (3% of all locations). Adults were found in the shallowest areas during May (1.5 m) and June (1.6 m), when spawning occurred. After spawning, the adult distribution shifted to slightly deeper water, and fish were located in areas with mean depths between 1.8 and 2.2 m during July through November. The mean depths where adults were located in spring (1.7 m) and summer (1.6 m) were significantly different ($\alpha = 0.05$) from the mean location depths in autumn (2.2 m) and winter (2.3 m).

Mean distance to shore for adults varied with season,

TABLE 2.—Seasonal and monthly mean ($\pm 95\%$ confidence interval) water depth at location sites (m) and distance to shore (m) recorded for radio-tagged subadult common carp in Clear Lake, Iowa, 2005–2006. Mean lake temperature ($^{\circ}\text{C}$) for each season or month is also shown. Within a column, seasonal means followed by the same letter are not significantly different ($P > 0.05$).

Month	Mean temperature ($^{\circ}\text{C}$)	Mean depth (m)	Mean distance to shore (m)
Apr	11.2 ± 0.4 z	1.3 ± 0.3 z	204 ± 61 z
May	15.7 ± 0.5 y	1.3 ± 0.2 z	201 ± 53 z
Jun	23.0 ± 0.2 x	1.2 ± 0.2 z	156 ± 34 z
Jul	25.1 ± 0.3 w	0.7 ± 0.1 y	136 ± 47 z
Aug	25.0 ± 0.2 w	0.8 ± 0.1 z,y	165 ± 119 z

paralleling mean depth trends (Table 1). Adults were located farthest from shore in January (607 m) during ice cover and were found nearest to shore in May (155 m) and June (175 m) during spawning. After spawning, adults moved farther from shore, where they were located at mean distances of 290–335 m during July through November. Adults were located significantly closer to shore in spring (209 m) and summer (198 m) than in winter (402 m) and autumn (335 m).

Subadults were located predominately in shallow areas (Table 2). Ninety percent of all subadult locations occurred in water less than 2 m deep. The mean depth of areas in which subadults were located was 1.3 m in April and gradually decreased as the summer progressed, reaching 0.7 m in July (Table 2). The mean depth of areas occupied by subadults in July was significantly different from the mean depths of areas occupied in April (1.3 m), May (1.3 m), and June (1.2 m) but was not significantly different from August depth (0.8 m).

Subadults exhibited little variation in mean distance to shore between months (Table 2). Mean distance ranged from 204 m in April to 136 m in July and was not significantly different between months.

Adults were aggregated during parts of January, February, June, and November, when mean core activity areas were smallest (Figure 2). During January and February, when ice cover was present, adults were commonly aggregated near the northern shore (Figure 3). During one tracking session, 21 of 30 adults (70%) were found in a tight aggregation in which all but two of the fish were within 50 m of another fish. As ice deteriorated in late February and early March, adults dispersed throughout the lake and remained so until prespawning activity in May (Figure 3). Adults also aggregated in May (Figure 3), but these prespawning aggregations were variable, resulting in a mean core activity area similar to that in April but with a larger

standard error (Figure 2). In early May, when lake temperatures warmed to 13°C, adults often were observed concentrating at the inlet where water from Ventura Marsh enters Clear Lake. Though passage was blocked by the gate, fish were seen leaping at the gate in an attempt to pass the barrier and enter the marsh. During the height of spawning in late May and early June, when water temperatures ranged from 18°C to 22°C, spawning fish were often observed breaching the surface in beds of emergent vegetation. Adults dispersed throughout the lake after spawning and remained dispersed until November (Figure 3). As lake temperatures cooled to 1°C in November, fish aggregated off the north shoreline, most arriving within a few days.

Subadults did not disperse as widely as adult fish but did show some tendency to aggregate in May and June (Figure 2). Subadult fish remained primarily in the lake's west end and were usually located in beds of emergent vegetation. Subadults dispersed during April but aggregated during a few tracking sessions in May and June (Figure 4). Subadult aggregations were usually found in beds of emergent vegetation but were also located near the inlet during periods of high flow. No aggregation was evident in July.

Habitat Selection

Adults did not use all habitat types in proportion to their availability ($P \leq 0.05$), demonstrating strong positive selection for shallow, vegetated habitats in all seasons (Figure 5). During winter, selection ratios for shallow, vegetated areas were 6.7 in 2005 and 8.7 in 2006. Adults displayed negative selection for shallow, sandy habitats in winter 2005 and deep, silty habitats in winter 2006. Adults showed the strongest selection for shallow, vegetated habitats during spring; selection ratios were 21.1 in spring 2005 and 23.4 in spring 2006. Adults also showed selection for shallow, silty areas during spring of both years, while avoiding middepth, silty habitats. During summer in both years, adults selected for shallow, vegetated areas. Middepth, silty habitats were used in proportion to availability during summer 2005 but were selected against during the subsequent year. Adults selected for shallow, vegetated habitats again in autumn, while demonstrating negative selection for shallow, sandy habitats. Adults were never located in deep, rocky habitats.

Subadults also demonstrated strong positive selection for shallow, vegetated areas; the selection ratio ranged from 48.0 in 2005 to 46.2 in 2006 (Figure 6). During both years, subadult fish used shallow, silty habitats in proportion to availability, while avoiding shallow, sandy areas. Subadults were never located in

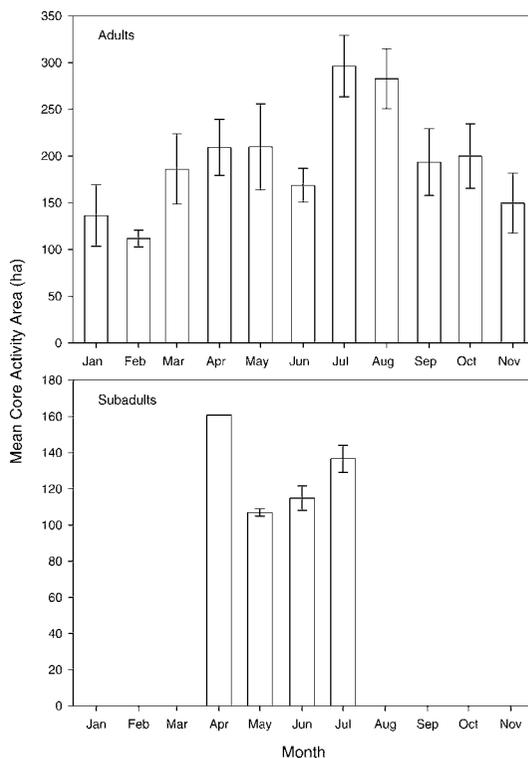


FIGURE 2.—Monthly mean (\pm SE) core activity area (ha) of adult (top panel) and subadult (bottom panel) common carp in Clear Lake, Iowa, 2005–2006. Smaller core activity areas indicate aggregation, while larger areas indicate dispersal.

middepth, rocky areas; deep, silty habitats; or deep, rocky areas.

Discussion

Our study, conducted year-round for over 22 months, demonstrated clear seasonal patterns in the distribution and aggregation of common carp in Clear Lake. Adult common carp were dispersed in the summer and were found predominantly in littoral habitats, whereas in winter they concentrated in deeper water. Otis and Weber (1982) observed that common carp in the Lake Winnebago system, Wisconsin, spent a majority of the summer occupying water that was 0.9–1.2 m deep and moved into slightly deeper areas (2.1 m) to overwinter. In Lake Banyoles, Spain, a much deeper system (mean depth = 14.8 m; maximum depth = 46.4 m), García-Berthou (2001) captured common carp at depths ranging from 0 to 20 m, but significantly more fish were caught in the littoral zone during the spring and in deep water during the winter. García-Berthou (2001) also noted a tendency to catch larger individuals in deeper habitats during winter. The trends we observed in adult common carp seasonal

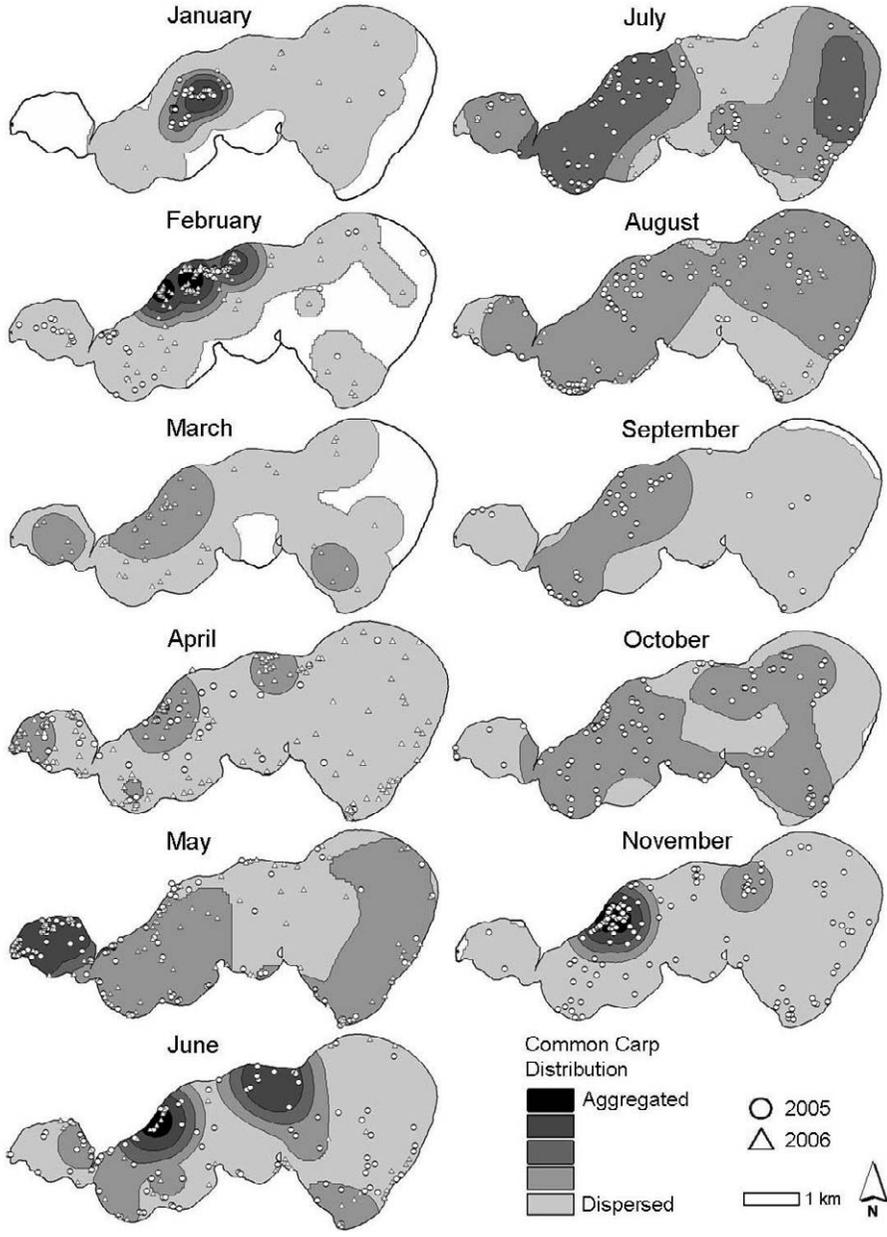


FIGURE 3.—Maps showing the monthly distribution of adult common carp in Clear Lake, Iowa, 2005–2006. Fish locations are indicated by symbols (circles = 2005; triangles = 2006); shading indicates probability contours (described in Methods) for adult distribution. The lightest shade represents a 95% probability contour; darker shades represent 70, 50, 30, and 10% probability contours and contain increasingly aggregated portions of the distribution.

depth and distance to shore in Clear Lake are consistent with those described in other lakes; these results collectively suggest that in many systems, common carp will be found primarily in littoral habitats during the spring and summer but will move to relatively deeper water to overwinter.

Subadult common carp occupied increasingly shallow areas as the summer months progressed, but there was no significant trend in distance to shore. These results are probably attributable to subadults staying in the same areas even as the water level receded due to decreased rainfall in late summer. Subadults in Clear

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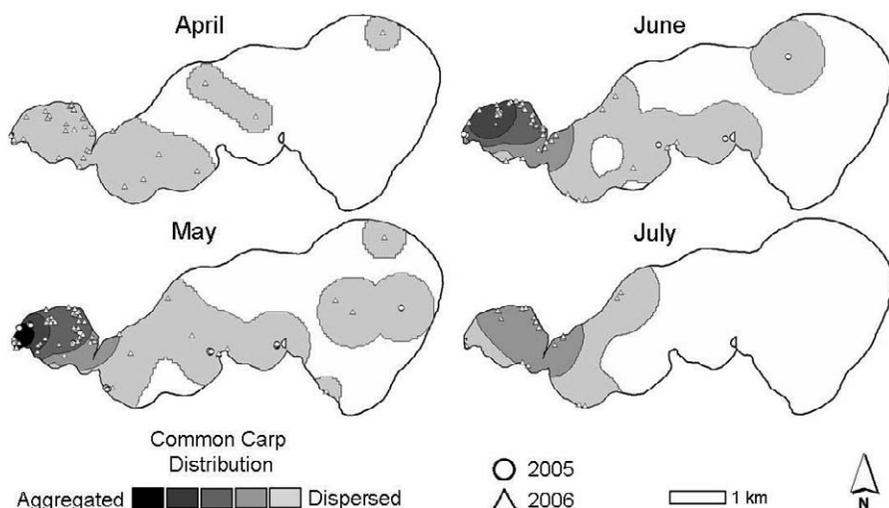


FIGURE 4.—Maps showing monthly distribution of subadult common carp in Clear Lake, Iowa, 2005–2006. Fish locations are indicated by symbols (circles = 2005; triangles = 2006); shading indicates probability contours (described in Methods) for adult distribution. The lightest shade represents a 95% probability contour; darker shades represent 70, 50, 30, and 10% probability contours and contain increasingly aggregated portions of the distribution.

Lake were located predominately in areas of 0.8–1.3-m depth and were rarely found outside beds of emergent vegetation. This is consistent with other studies reporting that common carp subadults are most abundant in shallow, vegetated areas (Bryan and Scarnecchia 1992; King 2004). In Spirit Lake, Iowa, subadults were caught significantly more often in areas with depths less than 1.5 m, where macrophytes were most abundant (Bryan and Scarnecchia 1992). Shallow, vegetated areas provide critical habitat for juveniles of many species and provide refuges where young fish can feed, grow, and avoid predation (Ridenhour 1960). Subadult common carp in Clear Lake probably use shallow, vegetated habitats as nursery areas until they reach a size at which the threat of predation is diminished.

Adult common carp in Clear Lake demonstrated a clear tendency to aggregate during periods associated with overwintering and spawning activity. Overwintering aggregations were observed at the same locations in November, January, and February of both years. Aggregations occurred in water from 2 to 4 m deep, either in proximity to beds of emergent vegetation or open water formed by turbulence from the lake's western aerator. Johnsen and Hasler (1977) reported that common carp in Lake Mendota, Wisconsin, formed large aggregations in areas on the edge of submerged macrophyte beds in 5–7 m of water. These aggregations were also observed in the same areas in multiple years and formed just before ice-up, when water temperatures dropped below 8°C. Winter aggre-

gations of common carp have also been reported in Lake Winnebago; Heron Lake, Minnesota; and the Grand River, Canada (Otis and Weber 1982; Verrill and Berry 1995; Brown et al. 2000). Similar overwintering behavior has also been reported in culture ponds. Bauer and Schlott (2004) observed that extensively cultured common carp restricted their use of culture ponds during ice cover to the same overwintering sites each year.

The cause or function of winter common carp aggregations remains unknown. Aggregation can increase survivorship (e.g., schooling) but can also be incidental and result from uneven resource distribution (Parrish and Edelstein-Keshet 1999). Theorized benefits of aggregation include predator avoidance (Smith 1997), increased foraging opportunities (Ryer and Olla 1991), hydrodynamic efficiency (Partridge et al. 1983), decreased metabolic activity (Parker 1973), and location of conspecifics before spawning (Johnsen and Hasler 1977). Studies from warmer regions lacking ice cover have not documented winter aggregations; this suggests that winter aggregations are due to low temperature, ice cover, or some combination of the two. While overwintering aggregations of common carp could serve some function, they could simply result from attraction to crucial winter habitat.

Spring aggregations of adults were also observed in association with spawning. Common carp are known to concentrate in potential spawning areas well before spawning occurs (Swee and McCrimmon 1966; Horvath 1985). Prespawning aggregations appeared

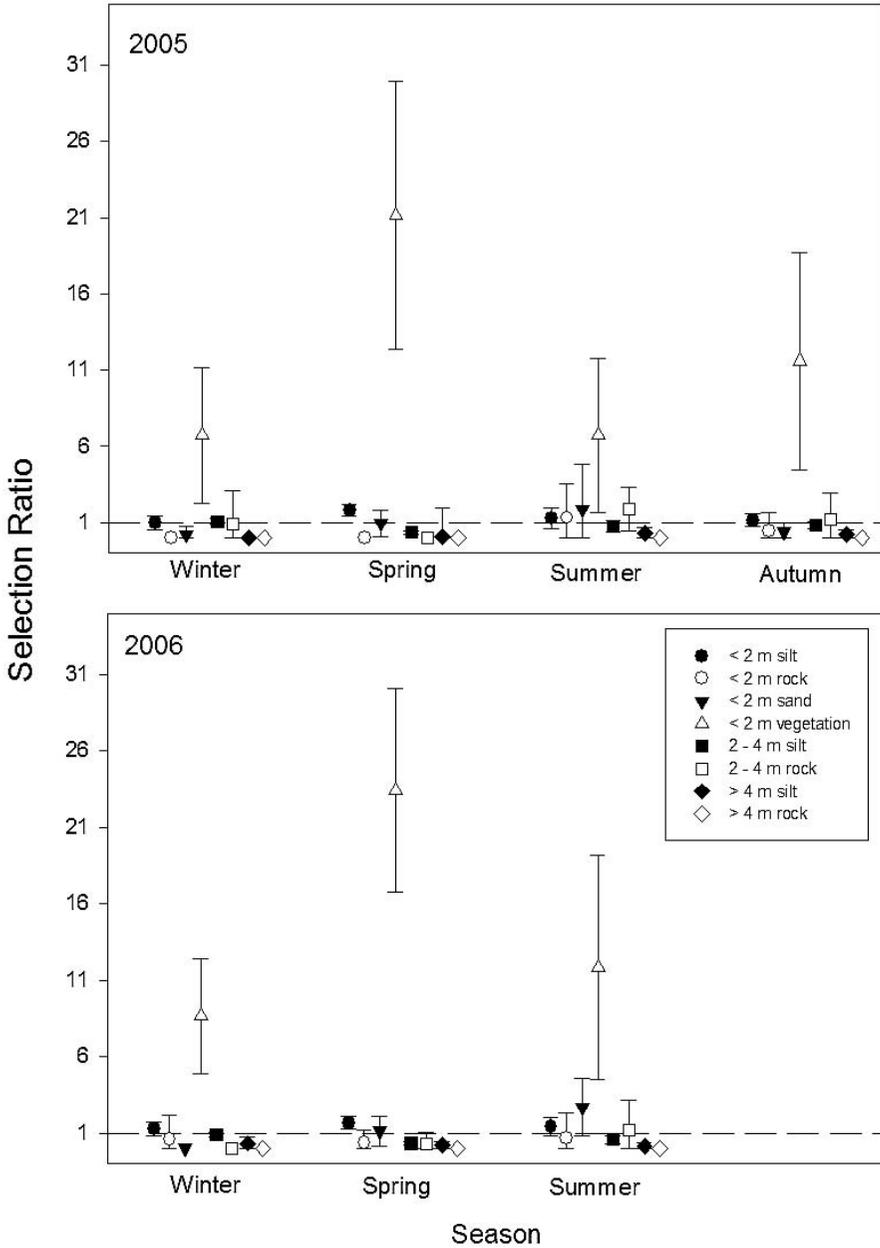


FIGURE 5.—Mean (\pm SE) seasonal habitat selection ratios (use : availability) calculated for radio-tagged adult common carp in Clear Lake, Iowa, 2005–2006. Values greater than 1.0 indicate positive selection for a particular habitat type (defined by depth, substrate, and presence of aquatic vegetation; see legend in bottom panel); values less than 1.0 indicate negative selection.

to be less stable than those formed during winter. Often, aggregations of adult fish in Clear Lake’s shallow west end were present during one tracking session and gone the next. Furthermore, adults exhibited the greatest mobility during this period, and some individuals moved up to 6.5 km between

consecutive tracking days. Common carp were observed spawning along several of the lake’s shorelines but were particularly concentrated in shallow areas containing emergent vegetation. Our results support previous reports that shallow areas with abundant macrophytes or inundated areas of terrestrial vegetation

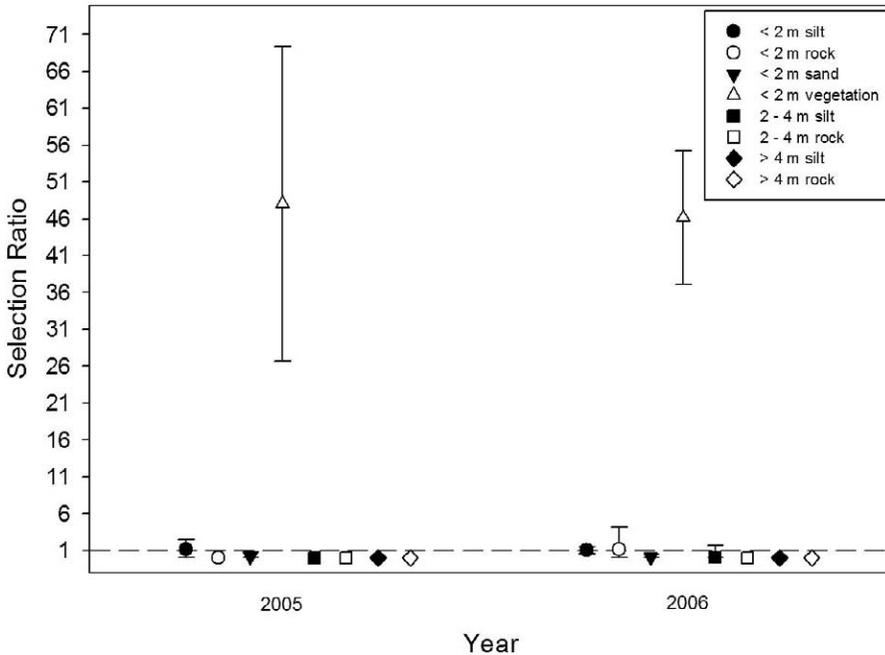


FIGURE 6.—Mean (\pm SE) seasonal habitat selection ratios (use : availability) calculated for radio-tagged subadult common carp in Clear Lake, Iowa, 2005–2006. Values greater than 1.0 indicate positive selection for a particular habitat type (defined by depth, substrate, and presence of aquatic vegetation); values less than 1.0 indicate negative selection.

(e.g., marshes, wetlands, and floodplains) are the preferred spawning habitat of common carp (Sweed and McCrimmon 1966; Loughheed et al. 1998; Stuart and Jones 2006).

Subadult common carp were observed aggregating during May and June in Clear Lake's western end. This apparent preference can be explained by the strong selection for shallow, vegetated areas, which are almost exclusively located in the lake's western half. In addition to beds of emergent vegetation, subadults also aggregated near the inlet but only when significant flow was present. Stuart and Jones (2006) observed large numbers of subadult common carp ascending a weir fishway in the Murray-Darling River, Australia; those authors suggested that in river systems, common carp will swim upstream and disperse into tributaries as soon as they attain a size that allows them to actively swim against a current. Although it is possible that the subadults we studied were attempting to return to the marsh from which they were collected, this attraction could also be an example of a more-general mechanism of common carp dispersal.

Throughout the year, common carp in Clear Lake demonstrated clear selection for shallow, vegetated areas. Subadult selection ratios for this habitat type were over twice the adult selection ratios, suggesting a shift in habitat use with ontogeny. This pattern is

consistent with that observed in the Broken River, Australia, where subadult common carp leave backwater nursery areas and move into pool and channel habitat as adults (Crook et al. 2001; King 2004). Other telemetry studies of adult common carp habitat use have described a range of vegetation use. Otis and Weber (1982) located common carp in vegetation over 94% of the time during summer months in Lake Winnebago. Alternatively, Crook et al. (2001) examined common carp habitat use at a range of scales in the Broken River and found a significant positive association with sandy habitat, a significant negative association with gravel habitat, and no association with vegetation. All previous information on subadult common carp habitat use suggests strong selection for vegetation, but this has been inferred primarily through correlations between local abundance and habitat variables (Sheaffer and Nickum 1986; Bryan and Scarnecchia 1992; Vilizzi and Walker 1999; Crook et al. 2001). While our findings are in agreement with studies using different methods, more studies of subadults are needed to fully understand their behavior, particularly in winter.

Understanding the ecology of common carp will be critical to the success of future control efforts. Our study demonstrated that common carp exhibit distinct, repeatable seasonal distribution and habitat selection patterns

that render the fish potentially vulnerable to a number of different control techniques, including mechanical harvest by netting (Fritz 1987; Pinto et al. 2005), water level manipulation to disrupt spawning (Summerfelt 1999), exclusion from spawning areas (Lougheed and Chow-Fraser 2001), localized piscicide application (Meronek et al. 1996), and electrical and behavioral barriers (Verrill and Berry 1995; Chick and Pegg 2001). In Clear Lake and other lakes with nuisance common carp populations, choice of appropriate control techniques will require consideration of efficiency, cost, and safety as well as social acceptability and prevailing regulations (Bomford and Tilzey 1997).

The demonstrated presence of common carp aggregations suggests that mechanical harvest by netting would be a potentially effective control strategy. Previous mechanical harvesting on East Okoboji Lake, Iowa, and Lake Wingra, Wisconsin, reduced common carp populations by up to 90% (Rose and Moen 1952; Neess et al. 1957). Our results demonstrated that the most compact, stable aggregations of common carp in Clear Lake occur in late fall and winter. Netting can be successfully performed under ice, but the increased effort required to set and retrieve nets reduces efficiency and increases costs. Further, winter aggregations of common carp in Clear Lake were located near thin ice created by turbulence from the lake's west aeration system, which creates an additional safety hazard. Thus, the best period for conducting mechanical harvest in Clear Lake is in late fall before ice formation.

Common carp exhibited selection for shallow, vegetated habitats during all seasons and showed a clear attraction to adjacent Ventura Marsh before the spawning period. These locations appear to function as spawning and nursery areas and are probably important for recruitment (McCrimmon 1963). Improving the barrier to fish passage in both directions between Ventura Marsh and Clear Lake should eliminate a potentially important source of recruits. Restriction of common carp from shallow, vegetated areas within the lake would further reduce recruitment and probably would have the additional benefit of enhancing the quality and extent of submersed vegetation (Lougheed et al. 1998; Schrage and Downing 2004). However, given the size and accompanying wave energy of Clear Lake, the extensive private development around the shoreline, and the popular use of the few vegetated areas for sportfishing, the feasibility of common carp exclusion from these vegetated areas is questionable.

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