2    Running head: *Residential development alters the spatial distribution of fishes*

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# Changes in the spatial distribution of fishes in lakes along a residential development gradient

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ABSTRACT

2     As the human demand for freshwater natural resources such as fish and drinking water

increases, we may rely more heavily on models to predict the response of aquatic ecosystems to

4    natural and anthropogenic disturbance. Theses models in turn implicitly depend on the

underlying spatial distribution of organisms. In terrestrial ecosystems, increased natural resource

6    utilization has transformed habitat and changed the spatial distribution of organisms, with

subsequent negative effects on biota. Recent studies in lakes demonstrate that human

8    development of lakeshores alters the physical habitat and nutrient cycles. The impact of such

disturbance by humans on the spatial distribution of aquatic organisms however, remains

10   unknown. Here we quantify the effect of lakeshore development on the spatial distribution of

fishes in 23 lakes in the U.S. Pacific Northwest. We found a significant decrease in the spatial

12   aggregation of fishes with increased shoreline development by humans, reflecting a loss of

refugia and resource heterogeneity that favor aggregation among fishes. We also found that lakes

14   with a high perimeter to surface area ratio and a relatively shallow littoral zone had much higher

levels of fish aggregation, suggesting the importance of terrestrial inputs to lakes. Finally, we

16   found a marginally significant decrease in fish spatial aggregation with increased total

phosphorus concentration, but no effect of chlorophyll concentration, water transparency, the

18   predator;prey ratio, or number of species on fish spatial distributions. These results suggest that

anthropogenic modification of shorelines is significantly altering the spatial distribution of

20   important aquatic organisms, and that these changes may have important implications for

predictive modeling of ecosystem dynamics.

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Key words: spatial distribution, lakeshore development, morphometry, model, hydroacoustics

INTRODUCTION

2          Humans increasingly impact the world's ecosystems through a variety of disturbances

such as changing land use, species introductions and extinctions, alteration of nutrient cycles,

4     and the use of >50% of the available fresh water (Vitousek et al. 1997). As the global human

population grows we will rely more heavily on aquatic resources for food, drinking water, and

6     recreation (Naiman et al. 1998, Naiman and Turner 2000, Jackson et al. 2001b). In light of these

increased demands, ecologists are challenged with making predictions about the response of

8     aquatic ecosystems to changes in the abiotic and biotic environment under a variety of natural

and anthropogenic disturbances (Pace 2001, Carpenter 2002). Central to these predictions are

10    models that incorporate predator feeding and prey mortality rates; these models depend

implicitly on the spatial distributions of interacting organisms. Furthermore, for simplicity these

12    models often assume that there is no systematic change in the spatial distribution of organisms

with human disturbance. Nevertheless, this critical assumption remains largely untested for

14    aquatic systems (Boisclair 2001), despite some evidence showing that human-mediated effects

can alter habitat use by fishes with cascading effects on lower trophic levels (Jeppesen et al.

16    2000, Olin et al. 2002). Furthermore, in terrestrial systems, anthropogenic habitat loss and

fragmentation has altered the spatial distribution of organisms, and changed competitive and

18    predator-prey interactions (Debinski and Holt 2000, Haila 2002).

          Lakeshores throughout North America and Europe are increasingly being developed and

20    altered by humans (Ostendorp et al. 1995, Christensen et al. 1996, Jennings et al. 1999,

Radomski and Goeman 2001, Beeton 2002, Gulati and van Donk 2002). Accompanying this

22    development are anthropogenic stresses to lake ecosystems including disruption of nutrient

cycles resulting in eutrophication (Jeppesen et al. 1997, Carpenter et al. 1998, Garrison and

Wakeman 2000, Moore et al. 2003) and changes in fish community composition (Jeppesen et al.

2    2000, Olin et al. 2002), introduction of exotic species (Jackson et al. 2001a), and the exploitation

of predatory fishes by recreational and commercial fisheries (Pauly et al. 2001, Post et al. 2002).

4    Furthermore, transformation of nearshore habitats adversely affects fish communities because

they form part of the physical template on which lake ecosystems lie (Jackson et al. 2001a,

6    Olden and Jackson 2001, Olden et al. 2001). Some direct impacts of lakeshore residential

development on the physical structure of lake habitats include bottom substrate modifications

8    (Beauchamp et al. 1994) and the removal of coarse woody debris (Christensen et al. 1996) and

aquatic vegetation (Ostendorp et al. 1995, Radomski and Goeman 2001). These habitat

10   modifications have been associated with a reduction of fish growth rates (Schindler et al. 2000),

altered trophic interactions (Jeppesen et al. 1997), and have the potential to alter fish spatial

12   distributions (Schindler and Scheuerell 2002).

Detecting changes in fish assemblages caused by human disturbance usually requires

14   observations before and after the disturbance (Lester et al. 1996), but such studies are often

protracted, expensive, and confounded by multiple time-dependent processes. We took an

16   alternative, comparative approach across lakes, which is useful in ecosystem studies where

experimental replication is impossible (Schindler 1998) and more rapid feedback is desired. To

18   evaluate the cumulative effect of lakeshore development on the spatial distribution of fishes, we

sampled 23 lakes in western Washington, USA, and southwestern British Columbia, Canada.

20   These lakes spanned a residential development gradient in the greater Seattle, WA metropolitan

area, which has a current human population near 2 million that grew almost 20% in the last 10

22   years. The intensity of lake shoreline disturbance by humans is highest near the Seattle urban

center and then generally decreases with distance from the urban area. Here we explored whether

human disturbance to lakeshores has any consequences for the spatial distribution of fishes. We

2     also examined the potential role of the lakes' physical morphology on fish spatial distributions

because of the natural interaction between morphology and physical habitat available to aquatic

4     organisms. Lakes with very steep sides have relatively little littoral habitat compared to pelagic

habitat (Wetzel 2001). Lakes with high perimeter to area ratios can receive relatively high inputs

6     of terrestrial matter compared to more circular lakes (Wetzel 2001). Finally, we compared the

relative role of cultural eutrophication (water clarity, total phosphorus and chlorophyll

8     concentrations), species diversity, and the ratio of predators to prey in explaining the observed

variance in fish spatial distributions.

10

METHODS

12          For our analyses, we considered two multiple regression models to explain the observed

variation in fish spatial distributions. Using backward stepwise regression, we began with the

14     following 8 predictor variables: housing density, shoreline morphometry ($D_L$), basin

morphometry ($D_V$), total phosphorus concentration, chlorophyll concentration, extinction

16     coefficient ($k$), the predator:prey ratio, and the number of species. Model 1 uses the number of

houses per km of shoreline whereas Model 2 uses the number of houses per ha of lake surface

18     area.

          **Lake data**. We sampled 10 of the lakes during 11-20 August 1998 and the other 13

20     during 23-31 August 1999. All of the study lakes were located in western Washington, USA, and

southwestern British Columbia, Canada, in a region east of Puget Sound and west of the Cascade

22     Mountains in an attempt to control for differences in geology, elevation, lake size, and

morphometry. Information on lake surface area, shoreline length, mean depth, and maximum

depth was obtained from the Washington State Lake Survey Data (Bortleson et al. 1976) and the

2    British Columbia Ministry of Sustainable Resource Management (http://www.gov.bc.ca/srm).

The elevation of all lakes ranged from 35–520 m above sea level. The average lake surface area

4    was 22 ha (± 3.4 SE), the mean depth across all lakes was 8.6 m (± 1.1 SE), and the average

maximum depth was 18 m (± 2.5 SE). All of the WA lakes had public access for boating and

6    fishing, but the BC lakes were located at the University of British Columbia Malcolm Knapp

Research Forest and therefore had neither public access nor shoreline development.

8          We used the number of nearshore houses per km of shoreline and the number of

nearshore houses per ha of lake area as general indices for the intensity of human disturbance.

10   We also chose three specific indicators of cultural eutrophication as potential predictors: 1)

hypolimnetic total phosphorus (TP) concentration ($\mu$g L$^{-1}$), 2) mean epi- and metalimnetic

12   chlorophyll a concentration ($\mu$g L$^{-1}$), and 3) the light extinction coefficient ($k$, m$^{-1}$). Lake water

was collected from depth using an 8 L Van Dorn bottle. Following persulfate digestion and

14   subsequent reaction with molybdate and stannous chloride, TP concentration was determined

colorometrically by reading the samples on a spectrophotometer at 720 nm and comparing them

16   to a standard curve (Anonymous 1999). Chlorophyll *a* concentration was determined by filtering

lake water through 0.7 $\mu$m GF/F glass-fiber filters, freezing them, extracting with methanol, and

18   then reading on fluorometer and correcting for pheophytins (Marker et al. 1980). Light was

measured at 1-m intervals using a Li-Cor Model 192SA light sensor. For each lake, we fit $k$ from

20   the standard equation for light extinction, where $L_z = L_0 \exp[-kz]$, $L_z$ is the amount of light at a

given depth $z$, and $L_0$ is the amount of light at the lake surface.

22         We chose two simple metrics to describe the physical morphology of our study lakes.

First, we used the volume development index ($D_V$) as a measure of the lake basin morphometry.

The index is expressed as the ratio of a lake's mean depth to its maximum depth (Wetzel 2001),

2    such that for a conical basin $D_V = 0.33$ and for a perfectly cylindrical basin $D_V = 1.0$. Second, we

used the shoreline development index ($D_L$) to classify the shape of the lake shoreline relative to

4    its area, where $D_L = 0.5P(\pi A)^{-0.5}$, $P$ is the length of shoreline, and $A$ is the lake surface area

(Wetzel 2001). For these purposes we adopt the convention of referring to $D_L$ as the shoreline

6    morphometry index to avoid confusion with our classification of the intensity of human shoreline

development.

8        **Fish data**. We obtained direct estimates of the fish community composition in each lake

with 10-12 unbaited minnow traps and 2 variable-mesh gill nets, set for approximately 2 hours.

10   The minnow traps had 0.25 inch mesh and were submerged in 0.5-2 m of water in the littoral

zone. Each gillnet was 33 x 2 m and consisted of five equal-area panels with bar mesh sizes of

12   1.3, 2.5, 3.8, 5.1, and 6.4 cm, and was set perpendicular to shore along the bottom. We gathered

additional information on the fish community composition from Washington Department of Fish

14   and Wildlife stocking and sampling records (http://www.wa.gov/wdfw) due to our low CPUE

presumably resulting from low fish densities and relatively short soak times. The fish community

16   was similar among all lakes and consisted of naturally reproducing and stocked populations of 1-

5 of the following species: largemouth bass (*Micropterus salmoides*), pumpkinseed sunfish

18   (*Lepomis gibbosus*), black crappie (*Pomoxis nigromaculatus*), yellow perch (*Perca flavescens*),

brown bullhead (*Ictalurus nebulosus*), rainbow trout (*Oncorhynchus mykiss*), or cutthroat trout

20   (*O. clarkii*).

We measured the three-dimensional locations of fish using a BioSonics DT6000 split-

22   beam echosounder operating at 200 kHz with an elliptical transducer consisting of -3 dB beam

angles of 6.7 and 13.5 degrees; the narrow beam was parallel to the direction of travel. We used

a 0.4 ms pulse at a rate of 4 s$^{-1}$ with the lower threshold set at -70 dB. Using the BioSonics

2   Visual Acquisition 4.0 software, all incoming signals were digitized at the transducer and then

stored on a computer hard drive for later analysis. The transducer was suspended from a pole

4   mount immediately under the water surface and towed alongside the boat at a speed of 10 km hr$^{-1}$

as the survey followed 8-14 predetermined transects across each lake over a total distance of

6   1300-4200 m (mean = 2500 ± 130 SE). Acoustic transects were selected non-randomly in an

effort to provide adequate survey coverage without biasing any particular depth contours,

8   embayments, docks, houses, etc. The total sample volume was 5800-160000 m$^3$ (mean = 30000

± 8300 SE). All hydroacoustic surveys occurred between 11:30 and 17:30. Fish density and the

10  depth and size of individual echoes were obtained using the BioSonics DT Analyzer 4.0

software, but we only analyzed depths <1 m due to near-field effects of the acoustic beam. For

12  these analyses we combined all potential prey fish together and classified all targets less than -46

dB as prey fish, which correspond to fish lengths <100 mm (Burczynski and Johnson 1986). All

14  subsequent analyses only refer to these small fishes. Densities of predator and prey fishes were

obtained by multiplying the total fish density by the proportion of all target strength values

16  within each class (prey < -46 dB; predators > -40 dB). We obtained simultaneous measurements

on the x-y coordinates of the fish by coupling the hydroacoustics to a sub-meter accurate

18  Trimble® AgGPS 132 differential global positioning system (DGPS).

We assessed the degree of spatial aggregation among fishes using a method developed

20  for three-dimensional point process patterns (Scheuerell 2002) based on the methodology for a

two-dimensional case (Coomes et al. 1999). This method involves measuring the locations of

22  individual organisms in three dimensions with hydroacoustics coupled to a differential global

positioning system (DGPS), and then calculating the nearest neighbor distances among

organisms. For each lake, we compared the observed cumulative probability ($G_{obs}$) of a fish

2    having a nearest neighbor within a given radius to that expected in a random distribution ($G_{PV}$)

assuming a three-dimensional Poisson process. We compared the two probability distributions

4    through the test statistic $dw_{obs}$, which equals the maximum difference between $G_{obs}$ and $G_{PV}$ over

all radii examined (0.2 - 5.0 m). This statistic therefore tests for aggregation over all spatial

6    scales within the range of radii considered (Coomes et al. 1999). We estimated the null

distribution of $dw$ by comparing $G_{PV}$ to $G_{obs}$ from 1000 Monte Carlo simulations of a three-

8    dimensional Poisson process. The critical values of $dw$ were then calculated from the upper tail

of the null distribution such that the 95th percentile indicated $dw_{crit}$ for $P = 0.05$ (sensu Coomes et

10   al. 1999). When the ratio of $dw_{obs}:dw_{crit} > 1$, the spatial distribution is significantly aggregated.

We used this ratio as a measure for the intensity of aggregation among fishes such that large

12   values indicate strong aggregation and values approaching zero are randomly distributed in

space. To account for sampling biases associated with the beam geometry, we distributed points

14   randomly within a large volume according to a three-dimensional Poisson process and then

sampled them using an artificial hydroacoustics beam using 500 Monte Carlo simulations. We

16   then calculated the edge correction as the mean difference between the observed $G_{PV}$ and the

expected $G_{PV}$ in an infinite universe (Coomes et al. 1999).

18

RESULTS AND DISCUSSION

20          Both human development of lakeshores and lake morphometry were related to the spatial

distribution of fishes (Table 1). In the stepwise multiple regression, housing density had the

22   strongest effect on the spatial aggregation of fishes, such that as housing density increased, the

spatial aggregation of fishes decreased (Figure 1A, 1B). This pattern held for either case when

we used the number of houses per km of shoreline or the number of houses per ha of lake surface

2    area, although the overall effect of houses per area was slightly more than that of houses per

shoreline (Table 1). Furthermore, in both cases the basin morphometry index ($D_V$) had the next

4    strongest impact (Table 1). $D_V$ had a negative effect on the degree of spatial aggregation among

fishes (Figure 1D), indicating that as the lake basin became more cylindrical in shape, fish

6    aggregation decreased. Once the ratio of mean depth to maximum depth reached 0.5, the fish

showed essentially no aggregation behavior. We also found a significant positive effect of

8    lakeshore morphometry ($D_L$) on the degree of spatial aggregation among fishes (Figure 1C),

demonstrating that fish were more aggregated in lakes with increasingly complex shorelines.

10    However, $D_L$ was only a significant predictor in the case where we used the number of houses

per shoreline, and in that case only marginally so (Table 1). Lakes with a high perimeter to area

12    ratio and a relatively shallow littoral zone may offer more habitat heterogeneity and refuge from

predation, which could subsequently affect the spatial distribution of fishes (Olden and Jackson

14    2001).

Of the cultural eutrophication variables we examined, only total phosphorus had a

16    significant effect on the degree of spatial aggregation among fishes, but it was relatively weak

and only occurred when we used houses per area as the metric for human disturbance (Model 2,

18    Table 1). The trend was for a decrease in fish spatial aggregation with increased TP

concentration (Figure 1E). Although it was not significant, increased chlorophyll concentration

20    also showed a pattern toward decreased aggregation (Figure 1F). This could suggest that

decreased water clarity associated with increased nutrients and algae also decreased fish

22    aggregation, as fish spatial distributions are often affected by light (Sogard and Olla 1993,

Miyazaki et al. 2000, Scheuerell and Schindler 2003). However, we found no relationship

between our direct measure of water clarity (*k*) and fish spatial aggregation (Figure 1G). On the

2     other hand, it might suggest that changes in the lower food web structure associated with

increased anthropogenic activities alter the spatial distribution of fishes through some sort of

4     bottom-up forcing associated with shifts in fish diets from predominantly benthic in undeveloped

areas to more pelagic in heavily impacted areas (Schindler and Scheuerell 2002). Predators often

6     exhibit strong effects on the spatial distribution of fishes (Werner and Gilliam 1984, Lima and

Dill 1990, Lima 1998). However, we failed to find any statistical relationship between the ratio

8     of predators to prey and the degree of spatial aggregation in our study lakes (Table 1, Figure 1H).

We also found no effect of the actual predator density on spatial aggregation (linear regression,

10    $R^2 = 0.094$, $P > 0.10$).

The density of organisms is implicitly coupled to their spatial distribution; as density

12    increases, the expected distance between neighbor's decreases. The average density of prey

fishes in the study lakes was 0.097 m$^{-3}$ ($\pm$ 0.024 SE) and the mean density of predatory fishes

14    was 0.0011 m$^{-3}$ ($\pm$ 0.00038 SE). Neither the density of prey fishes nor predatory fishes varied

across the residential shoreline development gradient (linear regression, prey: $R^2 = 0.005$, $P >$

16    0.10; predators: $R^2 = 0.0004$, $P > 0.10$). It is important to point out that the spatial statistic we

used (*dw*) explicitly accounts for the density of organisms, and is therefore robust to potential

18    biases associated with differences in fish density among lakes. We also found no significant

change in the mean acoustic target strength (i.e. fish size) with residential development (linear

20    regression, $R^2 = 0.15$, $P > 0.10$). The mean ($\pm$SE) number of fish caught per lake was 6.3$\pm$0.83

and 4.0$\pm$0.49 in the gillnets and minnow traps respectively, which was generally too low to

22    assign reasonable species identification to the acoustic density estimates. Therefore, we used the

trap and net data to assess species presence and community composition, and relied on the

2    hydroacoustics for fish density.

Human disturbance has been associated with changes in fish community composition in

4    streams (Vila-Gispert et al. 2002), wetlands (Brazner 1997), lakes (Jeppesen et al. 2000), and

nearshore marine environments (Guidetti et al. 2002). Differences in community composition

6    could affect the spatial distribution of fishes through predator-prey interactions (Brabrand and

Faafeng 1993) or other behavioral mechanisms (Olden and Jackson 2001). Although there were

8    subtle differences in the fish community composition among our study lakes (Figure 2), we

found no effect of the number of species on the spatial aggregation of fishes in a stepwise

10    multiple regression context (Table 1) or when we considered species number by itself (Pearson

correlation, $r = 0.062$, $P > 0.10$). Furthermore, we found no significant effects of the presence or

12    absence of any particular fish species on the spatial distribution of fishes (Kruskal-Wallis test, $H$

$= 4.2$, $P > 0.10$). Lastly, we found no difference in the mean number of fish species in lakes with

14    significant aggregation versus lakes without (Mann-Whitney test, $U = 91$, $P > 0.10$). This

suggests that the cumulative effects of humans and lake morphometry are more important than

16    the actual fish species assemblage in lakes such as these with relatively simple fish communities.

Our sampling design and methodology was somewhat biased toward the pelagic habitat

18    and deeper fish due to the cross-lake transects and the conical shape of the hydroacoustic beam.

However, there should not have been any systematic bias against any particular lake because

20    transects did not follow any specific depth contour, the length of which would differ among

lakes. Furthermore, we also note that our analysis of the sampled fish explicitly accounts for the

22    beam geometry and therefore doesn't introduce any bias associated with fish depth. Given the

possible bias toward pelagic habitats, our results using the number of houses per ha of lake

2    surface area may be more appropriate (Table 1, Model 2).

        Our comparisons relied on relatively simple, linear models to explain differences in the

4    spatial distribution of fishes. Certainly the ecological processes occurring throughout the lakes

vary spatially and are affected by a variety of internal and external processes (Turner and

6    Carpenter 1999). This observed variation may result from nonlinear interactions among

ecosystem components, such as predators and prey (De Roos and Persson 2002). Largemouth

8    bass were the dominant piscivore in our lakes, occurring in 15 of 23 lakes across a wide range of

human development intensity (Figure 2). Largemouth bass tend to be highly aggregated in

10    undeveloped lakes (Essington and Kitchell 1999), but that appears to change as lakes are

impacted by humans. Furthermore, human-mediated nutrient loading, habitat disturbance, and

12    exploitation can abruptly shift lakes to alternative stable states (Scheffer et al. 2001). Finally,

habitats within lakes are not isolated, but are instead connected via biotic and abiotic processes,

14    which are likely a function of the physical template (Schindler and Scheuerell 2002). Perhaps our

observed change in the spatial distribution of prey fishes resulted from nonlinear interactions

16    among their predators, human impacts, and lake morphometry.

        All natural populations demonstrate spatial and temporal variation in their numbers.

18    Some of this variability is associated with the physical structure of their habitat. For many years

terrestrial ecologists have paid particular attention to the role of human-mediated habitat

20    fragmentation in determining the distribution and interaction among species. These studies have

shown that changes in habitat structure often lead to subsequent variation in the spatial

22    distribution of organisms and that these changes must be considered when conserving or

restoring ecosystems (Debinski and Holt 2000, Fahrig 2002, Haila 2002). Only recently have we

begun to appreciate analogous anthropogenic disturbances in aquatic ecosystems. Evidence is

2  accumulating which shows that human development of lakeshores affects the physical habitat of

lakes and the fish community associated with it (Beauchamp et al. 1994, Christensen et al. 1996,

4  Jennings et al. 1999, Schindler et al. 2000, Jackson et al. 2001a, Olden and Jackson 2001,

Radomski and Goeman 2001). This study represents another step toward understanding the

6  negative effects of human disturbance on lake ecosystems by showing how the spatial

distribution of fishes changes with increased lakeshore development. We suspect that a

8  combination of eutrophication and associated water clarity (Jeppesen et al. 2000, Olin et al.

2002), changes in trophic structure associated with fish exploitation (Post et al. 2002) and

10  predation (Brabrand and Faafeng 1993), and degradation of nearshore habitats (Brazner 1997,

Schindler and Scheuerell 2002) all contribute to this response. Furthermore, direct disturbance by

12  swimmers and boaters could be perceived as a form of predation risk and alter fish spatial

distributions (sensu Frid and Dill 2002).

14      Researchers and managers alike often rely on empirical models of fish production,

nutrient cycling, or contaminant flows to predict the effect of human actions on lake ecosystems

16  (Carpenter and Gunderson 2001). For simplicity, these models often ignore or average spatially

explicit features of the biotic and abiotic environments. However, lakes are heterogeneous, three-

18  dimensional landscapes whose structure is influenced by physical, biological, and human

activities (Riera et al. 2001). Therefore, consideration of the underlying assumptions is critical

20  when a model is used to evaluate changes within or among ecosystems (Boisclair 2001). As an

example we show how lakeshore development changes the underlying spatial distribution of

22  fishes, which is usually assumed constant across systems. Most of the anthropogenic

disturbances to aquatic ecosystems associated with lakeshore development occur gradually over

time (Jennings et al. 1999), which should allow for proactive management in areas where

2    development of lakeshores is just beginning (Moore et al. 2003). In these cases, incorporating

knowledge about the interaction between humans and the environment will prove critical to

4    understanding and predicting ecosystem dynamics (Carpenter 2002). Given the wide-ranging

negative effects of anthropogenic habitat transformations on organisms in terrestrial ecosystems,

6    we suspect that similar effects are prevalent, but unexplored, in aquatic ecosystems.

ACKNOWLEDGMENTS

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Table 1. Results of the backward-stepwise multiple regression analyses to predict the spatial

2    aggregation of fishes. Both statistical models began with the following predictor variables:

housing density, shoreline morphometry ($D_L$), basin morphometry ($D_V$), total phosphorus

4    concentration, chlorophyll concentration, extinction coefficient ($k$), the predator:prey ratio, and

the number of species. Model 1 uses the number of houses per km of shoreline whereas Model 2

6    uses the number of houses per ha of lake surface area.

| Model | Variable | Coef. | SE | $t$ | $P$ | $r^2$ |
|-------|----------|-------|-----|-----|-----|-------|
| 1 | intercept | 3.1 | 1.8 | 1.8 | 0.096 | |
| | houses | -0.038 | 0.011 | -3.5 | 0.002 | 0.32 |
| | basin | -6.9 | 2.3 | -3.0 | 0.007 | 0.24 |
| | shoreline | 1.4 | 0.68 | 2.1 | 0.050 | 0.10 |
| | overall | | | | <0.001 | 0.66 |
| 2 | intercept | 6.7 | 1.1 | 6.4 | <0.001 | |
| | houses | -0.40 | 0.091 | -4.4 | <0.001 | 0.39 |
| | basin | -9.1 | 2.1 | -4.4 | <0.001 | 0.24 |
| | TP | -0.014 | 0.0080 | -1.8 | 0.088 | 0.09 |
| | overall | | | | <0.001 | 0.72 |

FIGURE LEGENDS

2

Figure 1. Relationship between the spatial aggregation of fishes and A) houses per km of

4        shoreline, B) houses per ha of lake surface area, C) shoreline morphometry index $D_L$,

D) lake basin morphometry index $D_V$, E) hypolimnetic total phosphorus concentration,

6        F) mean epi- and metalimnetic chlorophyll *a* concentration, G) light extinction

coefficient $k$, and H) the ratio of predators to prey (by density). The degree of spatial

8        aggregation equals the ratio of $dw_{obs}$ to $dw_{crit}$. Values >1 indicate significant

aggregation at $\alpha = 0.0022$ ($= 0.05/23$ comparisons). See methods for descriptions of

10        $D_L$, $D_V$, and $k$.


12 Figure 2. The total number of fish species and community composition for the 23 study lakes

ranked in order of increasing housing density (listed in parentheses, $km^{-1}$). See

14        methods for individual species names.


16