Box 2.6. Continued.

Next we construct the length, weight, and mortality structure of the population.

Table 2. Values of each variable for eight ages of black crappie. Explanation of variables follow table.

Age	1	2	3	4	5	6	7	8
TL	161	225	267	295	314	326	334	339
wt	0.13	0.40	0.72	1.00	1.22	1.39	1.51	1.59
V	0	0	1	1	1	1	1	1
lxfished	1.000	0.670	0.449	0.175	0.068	0.026	0.010	0.004

Total length in millimeters was estimated with the von Bertalanffy growth model, and weight (wt) in kilograms was estimated by the standard weight–length relationship for black crappie as $W = a \times TL^b$ (Anderson and Neumann 1996). The *V* (vulnerability) schedule was used to set the length and age at which fish become vulnerable to the fishery. In this case, we used an IF statement to set *V* equal to 0 if the mean length at that age was less than Reg and 1 if the mean length was equal to or larger than Reg. The row for "*lxfished*" is the survivorship per recruit in the fished condition, found by $lx_a = lx_{a-1} \times S_0 \times (1 - u \times V_{a-1})$, where lx_{a-1} was the survivorship from the previous age, S_0 is annual survival from natural mortality, u was the annual exploitation rate, and *V* is a vulnerability parameter that determines whether fish are vulnerable to *u* or not, per equation (2.15).

The Botsford incidence function of vulnerable biomass per recruit ($ø_{VB}$) was calculated as SUMPRODUCT(wt,*V*,*lxfished*). Yield per recruit was then found by $Y = u \times R \times ø_{VB}$, where *R* was the number of recruits. A second incidence function was set up as vulnerable number of fish per recruit, $ø_n$, by SUMPRODUCT(*V*,*lxfished*). Thus, total angler catch in numbers of fish was estimated as $C = u \times R \times ø_n$.

Table 3. Summary of Botsford incidence function values.

Vulnerable biomass per recruit ($ø_{VB}$)	0.64
Yield per recruit (YPR)	268.11
Vulnerable number per recruit ($ø_n$)	0.73
Catch per recruit (CPR)	307.69

To finish the analysis we simulated a range of exploitation rates and potential sizes of harvest (i.e., minimum length at harvest). We used the "Table" function in Excel to iterate the spreadsheet across a wide range of both values and show how equilibrium yield was predicted to change. See spreadsheet for instructions. The yield isopleth curve is shown below.

(Box continues)

Box 2.6. Continued.

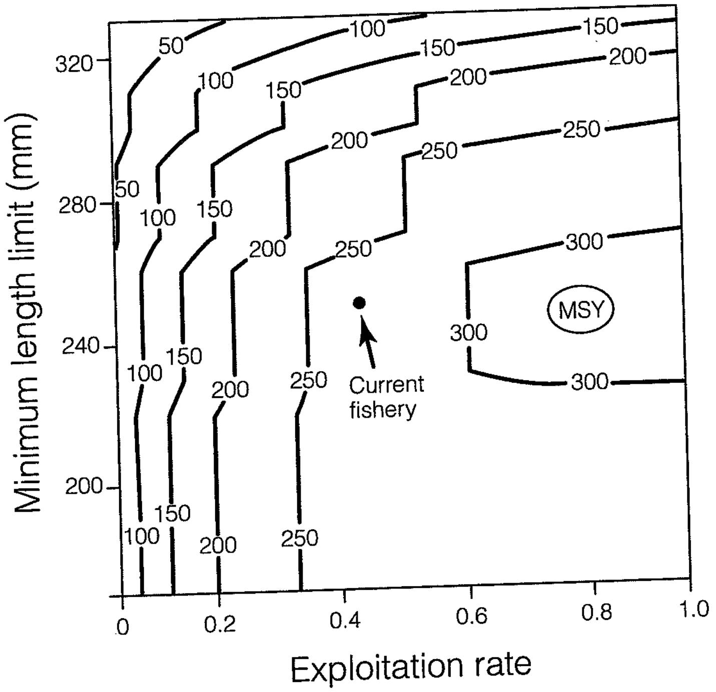

Figure. Yield isopleths (i.e., numbers in the plot represent yield in kilograms) for minimum length limit (*y*-axis) and exploitation rate (*u*, *x*-axis) combinations (MSY = maximum sustainable yield).

These yield isopleths (i.e., numbers within the plot represent yield in kilograms) show that the maximum sustainable yield (MSY) occurred at a minimum length limit of about 240–250 mm with annual exploitation rates of about 0.8. Growth overfishing was predicted to occur at *u* over about 0.6 if the minimum length at harvest was below 240 mm (notice the decline in yield if *u* was high [>0.80] and the minimum length limit dropped from 250 mm to 200 mm). This resulted because fish would be harvested before they reached the size that would maximize the yield. In this case the exploitation rate at Lake Dora was 0.42 (gray circle on plot). If the management objective was to maximize yield, increasing the exploitation rate would be recommended with about the same minimum length limit (250 mm TL). Establishing a minimum length limit above about 270 mm TL would cause declines in yield because many fish would die from natural mortality before reaching harvestable size. This example provides a way to construct YPR models to evaluate harvest policies in common recreational fisheries scenarios.

There are a variety of ways to estimate population abundance. For example, if a trawl is assumed to catch 100% of the fish in its path, the area swept by the trawl provides a measure of catch per unit area that can be used to estimate total abundance. Hydroacoustic sampling can provide estimates of total population abundance for certain species, depending on their vertical distribution (Brandt 1996). Capture–recapture methods can be effective in small systems such as streams or small lakes but are harder to apply in large lakes and rivers because of the difficulty in tagging and recapturing a sufficient fraction of the population. Overviews of capture–recapture methods can be found in Pine et al. (2003) and Hayes et al. (2007). One related approach that can be effective on larger systems is to use tagging in combination with a creel survey. Total harvest from the creel survey divided by the exploitation rate from the tagging program provides an estimate of absolute abundance.

An approach commonly used in large systems (e.g., large lakes) is to estimate the total harvest by age and then reconstruct the population from the catch-at-age matrix. This matrix of catches by age and year provides a record of removals from each cohort or year-class. The total catch from a cohort over its lifetime in the fishery is a minimum estimate of the initial size of that cohort. Correcting for natural deaths provides a better estimate of initial cohort size. Methods that attempt to recreate the stock abundance using historical catches are usually termed virtual population analysis (VPA).

An exceptional example of a catch-at-age dataset exists for the walleye *Sander vitreus* fishery at Lake Escanaba, Wisconsin, for the years 1956 to 1997 (Box 2.7). The entire catch-at-age matrix includes a few fish that were age 0 and older than age 12, but those have been omitted for this example. This lake is unique because anglers are required to report their entire catch when leaving the lake. Mandatory reporting has resulted in a high-quality dataset compared with the typical situation in which total harvest is estimated from a small subsample of catches. Walleye ages were determined from jaw tags and by examining scales. Catch sampling began in 1956, so age-1 fish caught in that year would be from the 1955 cohort (age 0 in 1955). Age-2 fish in 1956 are from the 1954 cohort. The earliest cohort in that year is the 1946 cohort at age 10. The most recent cohort that has completed its lifetime in the fishery is the 1985 cohort, which is age 12 in 1997. These completed cohorts are the simplest to analyze because it can be assumed that no fish from those cohorts remain (Hilborn and Walters 1992).

Estimates of age-1 abundance for the completed cohorts showed that recruitment has varied widely over time, from about 2,000 to 18,000 fish per year (Box 2.7). Strong and weak year-classes were apparent and can be tracked across years (e.g., the weak 1960 year-class is evident through at least age 6 in 1966). The ability to track strong and weak year-classes across years is a sign that the age data are reliable. The occasional strong year-classes (e.g., 1955, 1973, and 1981) can have a big impact on the population and result in several years of high catches. Slight modifications of the method shown here provide estimates for incomplete cohorts (Hilborn and Walters 1992), so that the catch-at-age matrix can be transformed into estimates of population size for every age and year. There are also statistically-based catch-at-age analyses that use the same information and produce similar results but provide estimates of the uncertainty in estimating population abundance and fishing mortality (Hilborn and Walters 1992; Quinn and Deriso 1999). These methods are beyond the scope of this chapter but are recommended for carrying out catch-at-age analyses.

Catch-at-age methods are dependent on an assumed value of natural mortality. Changing M produces a new set of population estimates that will be consistently higher or lower, depending on whether M is decreased or increased. Although absolute abundance will differ,

Box 2.7. Virtual Population Analysis

Table 1. Data based on catches of walleye by age (1–12) and year (1956–1997) from Escanaba Lake, Wisconsin (unpublished data, M. Hansen, University of Wisconsin–Stevens Point).

	Age											
Year	1	2	3	4	5	6	7	8	9	10	11	12
1956	702	2,247	448	309	492	97	129	23	11	1	0	0
1957	9	1,330	1,543	186	147	293	79	45	11	2	0	0
1958	1	26	452	462	49	36	108	29	13	5	0	0
1959	210	35	17	366	284	43	24	14	4	7	0	0
1960	736	553	58	28	581	336	38	7	14	1	1	7
1961	6	2,750	233	33	15	265	229	16	3	2	0	0
1962	27	34	1,869	111	20	61	134	225	8	0	0	0
1963	475	169	3	368	34	7	4	69	117	2	0	0
1964	428	963	122	6	112	11	23	25	28	34	1	0
1965	164	497	695	55	3	50	8	21	6	20	0	0
1966	73	1,739	389	328	35	5	61	96	7	5	0	27
1967	0	35	2,130	247	137	65	26	36	25	10	6	33
1968	2	175	220	371	141	37	26	14	12	12	0	0
1969	27	201	352	180	221	34	15	9	3	3	2	0
1970	164	682	430	454	181	198	33	9	6	2	2	7
1971	85	579	872	325	301	129	164	26	9	3	3	3
1972	41	131	171	223	157	25	16	16	12	5	1	2
1973	67	271	381	278	99	54	30	24	7	3	3	0
1974	112	121	239	193	213	71	61	38	13	12	3	3
1975	4	2,846	278	382	370	277	177	88	37	8	3	0
1976	38	789	1,801	345	133	171	116	60	32	16	7	2
1977	97	387	1,519	866	65	34	21	8	3	0	0	0
1978	120	625	749	1,178	468	93	38	24	9	3	0	0
1979	6	716	766	393	418	213	81	55	33	31	9	5

(Box continues)

Box 2.7. Continued.

Table 1. Continued.

Year	Age 1	2	3	4	5	6	7	8	9	10	11	12
1980	9	140	2,040	335	129	183	116	47	38	26	9	4
1981	77	496	144	539	80	22	24	13	2	5	0	0
1982	124	442	971	139	251	54	24	17	7	5	0	0
1983	8	1,495	283	450	101	241	37	18	15	6	1	1
1984	6	107	2,172	129	126	19	103	29	20	4	3	1
1985	17	101	348	1,960	54	31	21	43	12	6	3	2
1986	4	336	374	109	370	17	14	3	14	2	3	0
1987	64	567	1,734	370	61	90	16	9	0	1	0	0
1988	148	1,788	1,469	754	117	15	30	4	3	0	3	1
1989	37	622	2,804	577	165	27	10	12	3	0	0	0
1990	5	354	811	1,188	220	48	10	3	4	1	0	0
1991	8	52	415	300	208	23	10	2	2	1	0	2
1992	21	1,068	107	245	136	87	29	7	1	2	4	0
1993	8	137	998	138	174	97	68	14	10	8	1	2
1994	5	171	315	498	51	71	31	47	7	9	2	1
1995	40	135	525	277	216	31	28	28	17	1	1	0
1996	0	0	362	220	102	55	13	8	6	2	1	1
1997	0	0	1,952	298	111	50	30	4	5	6	6	1

Box 2.7. Continued.

Each cohort can be reconstructed by summing the catches and adjusting upward for natural mortality. Because natural deaths are not observed, the instantaneous rate of natural mortality (*M*) is often an assumed value based on the life history characteristics of that species. Here, a value of 0.4 is assumed.

The abundance estimate for each cohort begins at the oldest age and works backward. This is very convenient for cohorts that have completed their life in the fishery because it can be assumed that no fish from that cohort remain in the population. Abundance at the start of age 11 is the population abundance at age 12 (assumed to be the catch), adjusted upward for a year of natural mortality (simply divided by S_0 [e^{-M}]), plus the catch of age-11 fish that year. For the 1955 cohort, the expression would be

$$N_{11,\,1966} = N_{12,1967}/S_0 + C_{11,\,1966}.$$

The equation for the number at age 10 is

$$N_{10,\,1965} = N_{11,1966}/S_0 + C_{10,\,1965}.$$

A similar calculation is made for each age, working backwards up the diagonal to age 1.

(Box continues)

Box 2.7. Continued.

Table 2. Abundance estimates for each cohort of walleye from Escanaba Lake, Wisconsin.

	Age											
Year	1	2	3	4	5	6	7	8	9	10	11	12
1956	16,462											
1957	1,817	10,564										
1958	1,579	1,212	6,190									
1959	5,570	1,058	795	3,846								
1960	13,166	3,593	686	521	2,333							
1961	1,125	8,332	2,038	421	331	1,174						
1962	2,133	750	3,742	1,210	260	212	609					
1963	6,625	1,412	480	1,255	737	161	101	319				
1964	5,164	4,122	833	320	595	471	103	65	167			
1965	14,297	3,175	2,118	477	210	324	308	54	27	93		
1966	4,627	9,473	1,795	954	283	139	183	201	22	14	49	
1967	6,676	3,053	5,185	942	419	166	90	82	71	10	6	33
1968	6,826	4,475	2,023	2,047	466	189	68	43	31	31	0	0
1969	8,679	4,574	2,883	1,208	1,124	218	102	28	19	13	12	0
1970	8,690	5,799	2,932	1,696	689	605	123	58	13	11	6	7
1971	7,253	5,715	3,430	1,677	833	341	273	61	33	4	6	3
1972	5,675	4,805	3,443	1,715	906	356	142	73	23	16	1	2
1973	5,055	3,777	3,133	2,193	1,000	502	222	84	38	7	7	0
1974	17,344	3,343	2,350	1,845	1,284	604	300	129	41	21	3	3
1975	13,118	11,551	2,160	1,415	1,107	718	357	161	61	18	6	0
1976	5,823	8,790	5,835	1,262	693	494	295	121	49	16	7	2
1977	5,975	3,878	5,363	2,704	614	375	217	120	41	11	0	0
1978	12,928	3,940	2,340	2,577	1,232	368	229	131	75	25	7	0
1979	1,918	8,586	2,222	1,066	938	512	185	128	72	44	15	5
1980	5,796	1,282	5,275	976	451	348	201	69	49	26	9	4

(Box continues)

Box 2.7. Continued.

Table 2. Continued.

Year	Age 1	2	3	4	5	6	7	8	9	10	11	12
1981	2,540	3,879	765	2,169	430	216	111	57	15	7	0	0
1982	17,237	1,651	2,268	417	1,092	235	130	58	29	9	1	0
1983	2,135	11,471	810	869	186	564	121	71	28	15	2	1
1984	3,566	1,426	6,687	354	281	57	216	56	36	8	6	1
1985	8,989	2,386	884	3,027	150	104	25	76	18	10	3	2
1986	8,189	6,014	1,532	359	715	65	49	3	22	4	3	0
1987		5,486	3,806	776	168	231	32	23	0	5	1	0
1988			3,298	1,389	272	72	95	11	10	0	3	1
1989				1,226	426	104	38	43	4	4	0	0
1990					435	175	52	19	21	1	3	0
1991						144	85	28	11	11	0	2
1992							81	50	17	6	7	0
1993								35	29	11	2	2
1994									14	13	2	1
1995										5	2	0
1996											2	1
1997												1

The exploitation rate (u) can be estimated as the ratio of catch to population abundance (e.g., 702 / 16,462 for age-1 walleye in 1956). The instantaneous fishing mortality rate (F) is $-\log_e(1 - u)$, resulting in the following matrix of F estimates.

(Box continues)

Box 2.7. Continued.

Table 3. Instantaneous fishing mortality rate estimates for walleye from Escanaba Lake, Wisconsin.

	Age										
Year	1	2	3	4	5	6	7	8	9	10	11
1956	0.04										
1957	0.00	0.13									
1958	0.00	0.02	0.08								
1959	0.04	0.03	0.02	0.10							
1960	0.06	0.17	0.09	0.06	0.29						
1961	0.01	0.40	0.12	0.08	0.05	0.26					
1962	0.01	0.05	0.69	0.10	0.08	0.34	0.25				
1963	0.07	0.13	0.01	0.35	0.05	0.04	0.04	0.24			
1964	0.09	0.27	0.16	0.02	0.21	0.02	0.25	0.49	0.18		
1965	0.01	0.17	0.40	0.12	0.01	0.17	0.03	0.50	0.25	0.24	
1966	0.02	0.20	0.24	0.42	0.13	0.04	0.40	0.65	0.38	0.44	0.00
1967	0.00	0.01	0.53	0.30	0.40	0.50	0.34	0.58	0.44		
1968	0.00	0.04	0.12	0.20	0.36	0.22	0.48	0.40	0.49	0.50	
1969	0.00	0.04	0.13	0.16	0.22	0.17	0.16	0.39	0.17	0.27	0.18
1970	0.02	0.13	0.16	0.31	0.30	0.40	0.31	0.17	0.64	0.20	0.37
1971	0.01	0.11	0.29	0.22	0.45	0.48	0.92	0.56	0.32	1.10	0.70
1972	0.01	0.03	0.05	0.14	0.19	0.07	0.12	0.25	0.73	0.37	
1973	0.01	0.07	0.13	0.14	0.10	0.11	0.15	0.33	0.20	0.51	0.51
1974	0.01	0.04	0.11	0.11	0.18	0.13	0.23	0.35	0.39	0.85	
1975	0.00	0.28	0.14	0.31	0.41	0.49	0.68	0.79	0.94	0.57	0.70
1976	0.01	0.09	0.37	0.32	0.21	0.42	0.50	0.69	1.07		
1977	0.02	0.11	0.33	0.39	0.11	0.10	0.10	0.07	0.08	0.00	
1978	0.01	0.17	0.39	0.61	0.48	0.29	0.18	0.20	0.13	0.13	0.00
1979	0.00	0.09	0.42	0.46	0.59	0.54	0.58	0.56	0.62	1.20	0.92
1980	0.00	0.12	0.49	0.42	0.34	0.74	0.86	1.13	1.51		

(Box continues)

1980 0.00 0.12 0.49 0.42 0.34 0.74 0.86 1.13 1.51

(Box continues)

Box 2.7. Continued.

Table 3. Continued.

	Age										
Year	1	2	3	4	5	6	7	8	9	10	11
1981	0.03	0.14	0.21	0.29	0.21	0.11	0.24	0.26	0.14	1.18	
1982	0.01	0.31	0.56	0.41	0.26	0.26	0.20	0.35	0.27	0.85	0.00
1983	0.00	0.14	0.43	0.73	0.78	0.56	0.36	0.29	0.78	0.51	0.51
1984	0.00	0.08	0.39	0.45	0.59	0.41	0.65	0.72	0.82	0.64	0.70
1985	0.00	0.04	0.50	1.04	0.44	0.35	1.74	0.83	1.07	0.85	
1986	0.00	0.06	0.28	0.36	0.73	0.30	0.34		1.00	0.64	
1987		0.11	0.61	0.65	0.45	0.49	0.69	0.49		0.20	0.00
1988			0.59	0.78	0.56	0.24	0.38	0.47	0.37		
1989				0.64	0.49	0.30	0.31	0.32	1.10	0.00	
1990					0.71	0.32	0.22	0.17	0.21		0.00
1991						0.17	0.13	0.07	0.21	0.09	
1992							0.44	0.15	0.06	0.43	0.85
1993								0.51	0.42	1.30	0.51
1994									0.69	1.23	
1995										0.24	0.51
1996											0.51

It is not possible to estimate F for the last nonzero catch for a cohort. Notice that values of F increase across ages 1–4 for each year as fish grow and become more vulnerable to angling. The fishing mortality rates can be viewed across years, as desired for management (see figure below). This analysis suggested that fishing mortality varied widely from 1965 to 1986 but also showed a general increase through time.

(Box continues)

Box 2.7. Continued.

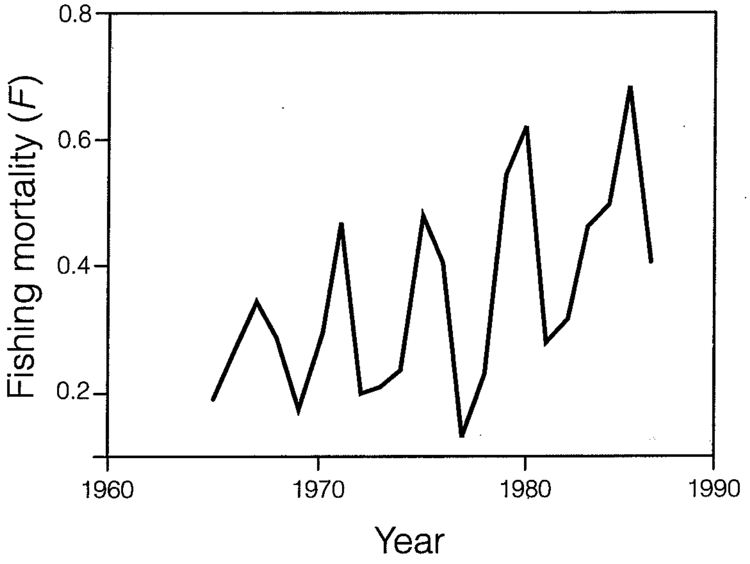

Figure A. Fishing mortality of walleye from 1965 to 1986 in Escanaba Lake, Wisconsin.

Other useful results from a virtual population analysis (VPA) include population abundance (totaled across all ages) and annual recruitment to age-1 (shown below). Notice how the strong and weak year-classes are evident simply by reconstructing the cohorts in the VPA.

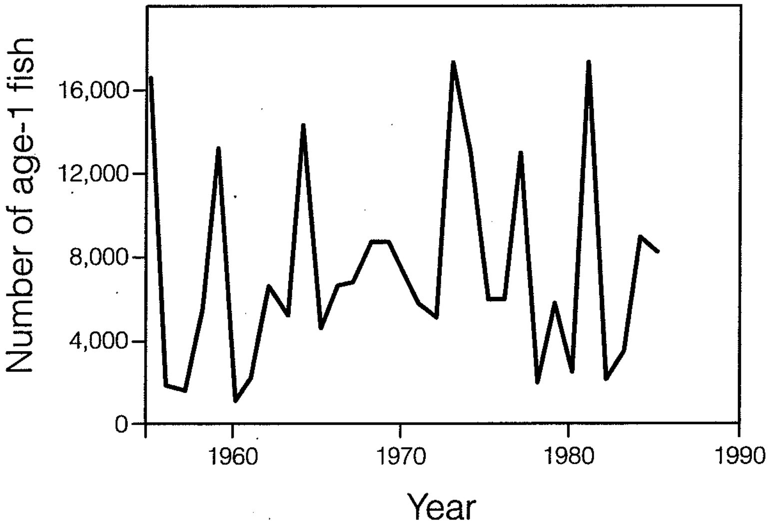

Figure B. Annual recruitment of age-1 walleye at Escanaba Lake, Wisconsin.

Population biomass can also be calculated by multiplying each abundance estimate by the associated average weight-at-age value.

the trend and year-to-year variability in year-class strength will be similar for different assumed values of *M*. Field studies to estimate *M* (e.g., a tagging study) can be used to reduce this source of uncertainty.

Catch-at-age models are routinely used in marine fisheries, but they have not been commonly used in freshwater systems other than the Great Lakes. They require more effort than do relative abundance surveys, but they can be derived from creel survey data if accompanied by estimates of age composition of the angler catch. The abundance estimates provide a strong foundation for single-species or multispecies models and are superior to relative abundance data for selecting an appropriate harvest rate.

2.5 CONCLUSIONS

Fisheries management requires making choices about harvest regulations, fish stocking programs, and habitat restoration Those choices influence fisheries resources and the human users who benefit from those resources. Estimating fish population parameters including mortality, growth, and recruitment and integrating those estimates into simple population models improves understanding of the factors influencing fish abundance and angler harvest. The methods outlined in this chapter serve as a first step towards proficiency in assessment of fish populations. Quantitative analysis of fish populations will always be a critical element for effective management, and the purpose of this chapter has been to show that most analyses are not difficult to draw basic fishery conclusions needed in most instances. When combined with effective use of harvest restrictions and other management strategies related to fish habitat and species composition, quantitative fisheries assessment methods will inform management decisions and improve fisheries in the future.

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