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Are Current Prevalence Rates of Ichthyophonus Consistent with High Natural Mortality?

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Abstract

A simple two stage model is used to describe the prevalence of Ichthyophonus in Georges Bank yellowtail flounder. The dynamics of healthy and infected individuals are modeled as functions of two key parameters. The first is the rate of new infections, denoted as ϕ, and the lethality of the disease, denoted as M2. The lethality of Ichthyophonus is based on the median survival times for infected animals. Results suggest that the observed prevalence rate of 2.55% is consistent with a low rate of new infections and high lethality (M2>4). When F is low, say ~0.1, the high lethality of the disease could result in total mortality from natural causes exceeding fishing mortality be a factor of 4. However as fishing mortality increases, the ability to attribute high losses due to M2 greatly diminishes, irrespective of the lethality of the disease or infection rate. Experimental data on the lethality of Ichthyophonus in yellowtail flounder are needed. Empirical information on the infection rate for new fish is also needed. Finally, since the prevalence rates of Ichthyophonus may not be higher that earlier historical estimates, one has to explain why the current rates of prevalence would be so lethal.

Introduction

The consequences of disease in a population depend on the rate of acquisition of the disease and the lethality of the disease once it is acquired. The potential consequences of Ichthyophonus on yellowtail flounder were explored using a simple two stage model in which fish can be in one of two states: healthy and infected. The dynamics of the healthy stock depend on the rate of fishing (F) and natural mortality (M1) (other than disease) and the rate of recruitment (R). It is assumed that recruitment is independent of stock size and that all new recruits are disease free. Healthy animals that acquire Ichthyophonus transition to the infected state. The dynamics of the infected population depend fishing (F) and natural mortality (M1) plus the mortality from disease (M2). The ratio of observed diseased to healthy fish is called the prevalence rate in this report. The reliance of the prevalence rate on the prevailing natural and fishing mortality rates, infection rate and lethality of the disease were examined in this report. Analytical expressions are derived for the equilibrium consequences of various parameter variations for abundance and total mortality. The veracity of the equilibrium expressions were checked with long term projections.

Methods

Let $N_{h,t}$ represent the population of healthy fish at time t. The abundance of fish at time $t+\Delta t$ can then be written as $N_{h,t+\Delta t}$. Fish are lost from the healthy population due to total mortality (i.e., $F+M1$) and those fish which acquire the disease at the infection rate ϕ. New fish which enter the population at time t are denoted as Rt.

The dynamics of the healthy stock can be written as

$$N_{h,t+\Delta t} = N_{h,t}e^{-Z\,\Delta t} - \varphi N_{h,t}e^{-Z\,\Delta t} + R_t \qquad (1)$$

Where Z=F+M1.

The infected stock grows as formerly healthy acquire the disease at a rate denoted as ϕ.

$$N_{i,t+\Delta t} = N_{i,t}e^{-(Z+M2)\,\Delta t} + \varphi N_{h,t}e^{-Z\,\Delta t} \qquad (2)$$

The prevalence rate is defined as the fraction of diseased fish in the population γ_t or

$$\gamma_t = \frac{N_{i,t}}{N_{i,t}+N_{h,t}} \qquad (3)$$

At equilibrium there is no change in the number of healthy fish per unit time such that $N_{h,t+\Delta t} = N_{h,t} = N_{h,e}$. We further assume that $R_t=R_e$. For Eq. 1 this implies that

$$1 = e^{-Z\,\Delta t} - \varphi e^{-Z\,\Delta t} + \frac{R_t}{N_{h,e}}$$

Solving for $N_{h,e}$ we find

$$N_{h,e} = \frac{R_e}{(1-e^{-Z\Delta t})(1-\varphi)} \qquad (4)$$

The infected population can be analyzed in the same way such that $N_{i,t+\Delta t} = N_{i,t}=N_{i,e}$. Dividing both sides of Eq. 2 by $N_{i,e}$ reveals the equilibrium population of infected fish to be

$$1 = e^{-(Z+M2)\Delta t} + \varphi\frac{N_{h,e}}{N_{i,e}}e^{-Z\,\Delta t} \qquad (5)$$

Solving Eq. 5 for $N_{i,e}$ gives

$$N_{i,e} = \frac{\varphi N_{h,e}e^{-Z\,\Delta t}}{1-e^{-(Z+M2)\Delta t}} \qquad (6)$$

Substituting Eq. 4 into Eq. 6 can be used to express the equilibrium number of infected fish as a function of the rate of recruitment, the infection rate ϕ, and lethality of the disease M2. With a little math, Eq. 6 becomes

$$N_{i,e} = \frac{[\varphi e^{-Z\Delta t}]\frac{R_e}{(1-e^{-Z\Delta t})(1-\varphi)}}{1-e^{-(Z+M2)\Delta t}} \tag{7}$$

The equilibrium catches and losses due to fishing, natural and disease sources can now be written as functions of the equilibrium stock sizes using the Baranov catch equation.

The equilibrium catch of healthy fish is expressed as

$$C_h = \frac{F}{Z}(1 - e^{-Z\Delta t})\frac{R_e}{(1-e^{-Z\Delta t})(1-\varphi)} \tag{8}$$

Substituting Eq. 7 into the catch equation give the equilibrium catch of infected fish as

$$C_i = \frac{F}{Z+M2}\left(1 - e^{-(Z+M2)\Delta t}\right)\frac{[\varphi e^{-Z\Delta t}]\frac{R_e}{(1-e^{-Z\Delta t})(1-\varphi)}}{1-e^{-(Z+M2)\Delta t}} \tag{9}$$

The equilibrium losses due to natural and disease related mortality can now be expressed as L(M) and L(M2), respectively. Natural mortality causes losses in both the healthy and infected populations such that

$$L(M1) = \frac{M}{Z}\left(1 - e^{-(Z\Delta t}\right)N_h + \frac{M}{Z+M2}\left(1 - e^{-(Z+M2)\Delta t}\right)N_i \tag{10}$$

Mortality due to disease L(M2) arises only from infected fish and can be expressed as

$$L(M2) = \frac{M2}{Z+M2}\left(1 - e^{-(Z+M2)\Delta t}\right)N_i \tag{11}$$

Equations 8 to 11 can be used to investigate the potential losses of yellowtail flounder over a range of assumed infection rates and lethality rates.

The lethality of the disease can be expressed as a function of the median survival time δ for infected individuals. Median survival time is the estimated time for half of the initial population to die following infection.

$$0.5 = \mathrm{e}^{-\mathrm{M2}\delta/365}$$

$$M2 = \frac{-\ln(0.5)}{\delta/365}$$

For example a median survival time of 105 days would correspond to an instantaneous rate of mortality of 2.41 whereas a median survival time of 10 days would imply M2=25.3.

Results

Observed rates of Ichthyophonus in the Georges Bank yellowtail population were about 2.55% (Huntsberger and Smolowitz 2014). The response surface of the prevalence rate γ vs the median survival time (i.e. M2=f(δ)) and the infection rate ϕ suggests the 2.55% prevalence rate is consistent with M2~4 (i.e., median survival times<63 d) when the infection rate ϕ is 0.01 and M2~20 (i.e., median survival time ~13 d) when the infection rate ϕ is 0.025.

The effects of this range of parameters combinations are shown in the table below:

Median Survival time (δ)	Nat Mortality due to disease M2	Infection Rate ϕ	Nat Mortality Base M1	Fishing Mortality Rate F	Prevalence Rate γ	Ratio of deaths from Natural Mortality to deaths from fishing mortality
63	4.01	0.0095	0.2	0.2	0.025	1.44
63	4.01	0.0095	0.2	0.1	0.026	2.91
63	4.01	0.0095	0.2	0.5	0.023	0.56
13	19.46	0.025	0.2	0.2	0.025	2.11
13	19.46	0.025	0.2	0.1	0.025	4.25
13	19.46	0.025	0.2	0.5	0.058	0.83

Results suggest that prevalence rates of about 0.0255 could be responsible for about 1.4 to 4.3 times the fishing mortality rate IF the lethality of the disease is high, corresponding to median survival time of between 13 to 63 days and an infection rate of between 0.01 and 0.025. At higher levels of fishing mortality, the prevalence rate declines slightly when M2~4.01 but the ratio of deaths due to natural mortality (L(M1)+L(M2)) fishing compared to fishing mortality drops to 0.56. Similarly, the last line in the above table suggests that high rates of lethality (M2) and modest infection rates (0.025) are inconsistent with high F because the prevalence rate rises to more than twice the observed rate. Moreover, the importance of disease as a primary driver of total mortality diminishes.

Tables 1 and 2 summarize the predicted prevalence rates for varying combinations of lethality (M2) and infection rates for base conditions in which M1=0.2 and F=0.1 (Table 1) or F=0.2 (Table 2). Table 3 illustrates how total yield declines as the infection rate ϕ increases but the lethality has a negligible effect. Similarly, the infection rate ϕ has a larger impact on the losses due to natural mortality than the lethality of the disease (Table 4). As ϕ controls the rate of transfer from the healthy to the infected population, it controls the flux from the larger pool of healthy fish, which in this case is sustained by regular recruitment of new individuals ***R.***

Discussion

This paper describes the mathematics of disease using a simple equilibrium model. It is meant to be a starting point for a discussion about the potential role of disease as a potential cause of high rates of natural mortality. Certain combinations of parameters for the lethality of Ichthyophonus and the infection rate of new individuals could lead to high losses due to disease. The plausibility of these rates of infection and lethality needs to be discussed. Moreover, since the prevalence rates of Ichthyophonus may not be higher that earlier historical estimates, one has to explain why the current rates of prevalence would be so lethal.

Reference

Huntsberger, C. and R. Smolowitz. 2014. Prevalence of *Ichthyophonus sp.* in yellowtail flounder sampled during the seasonal bycatch survey on Georges Bank TRAC Working Paper 2014/31

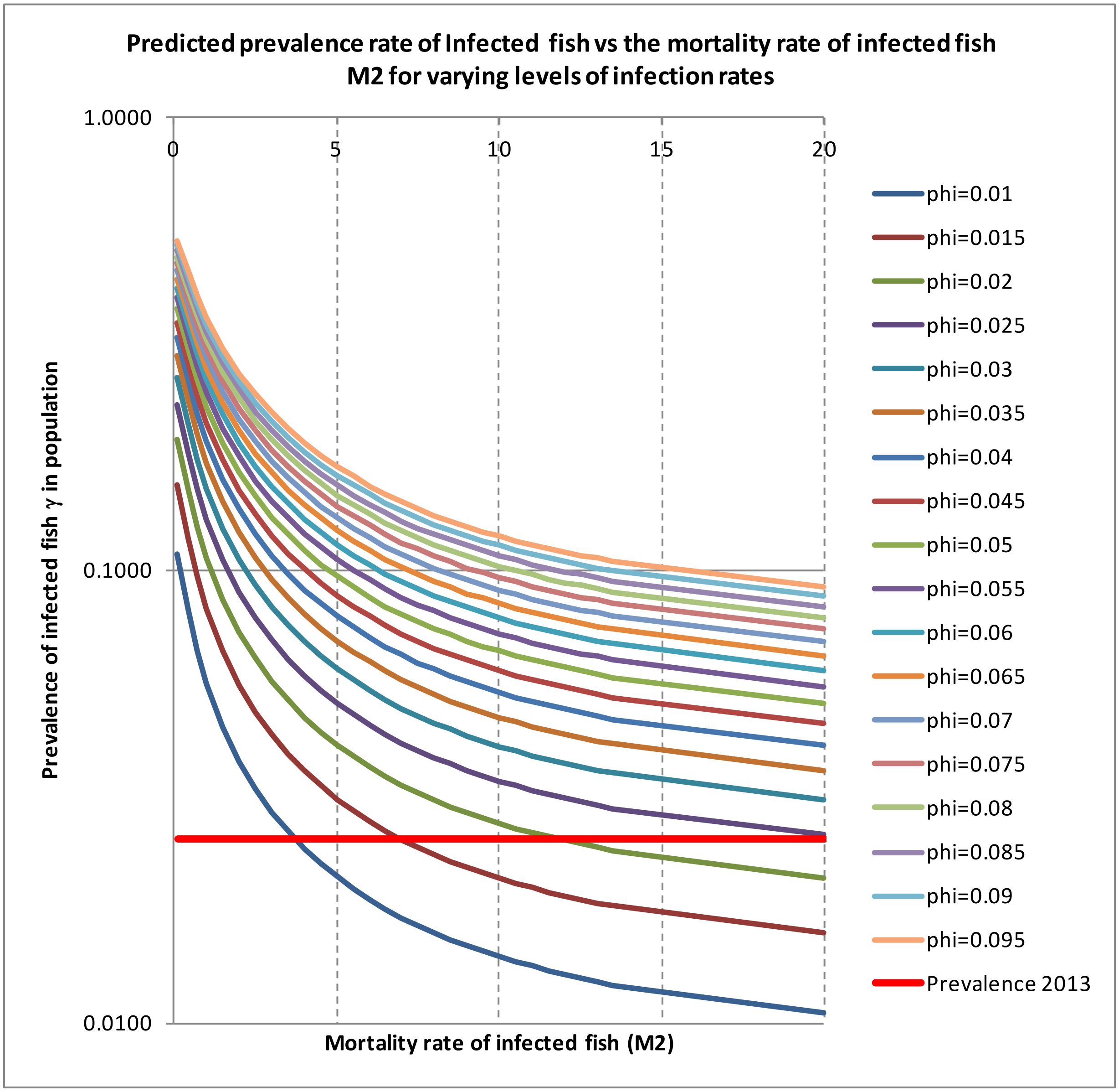

Figure 1. Predicted equilibrium prevalence rate γ as a function of the lethality of the disease M2 at varying levels of infection rates ϕ. Results suggest that the 2.55% prevalence rate is consistent with M2~4 (i.e., median survival times<63 d) when the infection rate ϕ is 0.01 and M2~20 (i.e., median survival time ~13 d) when the infection rate ϕ is 0.025.

Table 1. Summary of predicted prevalence rates for Ichthophonus for varying levels of median survival time δ and infection rates ϕ. The natural mortality rate for all other causes is assumed to be 0.2 and the fishing mortality rate is assumed to be 0.1.

Median Survival Time (d)	M2	phi=0.01	phi=0.015	phi=0.02	phi=0.025	phi=0.03	phi=0.035	phi=0.04	phi=0.045	phi=0.05	phi=0.055	phi=0.06	phi=0.065	phi=0.07	phi=0.075	phi=0.08	phi=0.085	phi=0.09	phi=0.095	Observed Prevalence 2013
2530	0.1	0.1984	0.2707	0.3311	0.3822	0.4261	0.4642	0.4975	0.5269	0.5531	0.5765	0.5976	0.6167	0.6340	0.6499	0.6644	0.6778	0.6902	0.7016	0.0255
632	0.4	0.1255	0.1772	0.2231	0.2641	0.3010	0.3344	0.3647	0.3924	0.4178	0.4412	0.4627	0.4827	0.5012	0.5184	0.5345	0.5496	0.5637	0.5769	0.0255
361	0.7	0.0925	0.1327	0.1694	0.2032	0.2343	0.2630	0.2897	0.3146	0.3377	0.3593	0.3796	0.3986	0.4165	0.4334	0.4493	0.4643	0.4786	0.4921	0.0255
253	1	0.0737	0.1067	0.1373	0.1660	0.1928	0.2179	0.2415	0.2637	0.2847	0.3045	0.3232	0.3410	0.3578	0.3738	0.3891	0.4036	0.4174	0.4306	0.0255
169	1.5	0.0556	0.0812	0.1054	0.1284	0.1502	0.1709	0.1907	0.2095	0.2275	0.2447	0.2612	0.2769	0.2920	0.3064	0.3203	0.3337	0.3465	0.3588	0.0255
126	2	0.0451	0.0662	0.0863	0.1056	0.1241	0.1419	0.1589	0.1753	0.1910	0.2062	0.2208	0.2349	0.2485	0.2616	0.2742	0.2865	0.2983	0.3097	0.0255
101	2.5	0.0382	0.0563	0.0736	0.0904	0.1065	0.1221	0.1371	0.1517	0.1658	0.1794	0.1925	0.2053	0.2176	0.2296	0.2412	0.2525	0.2634	0.2740	0.0255
84	3	0.0334	0.0492	0.0646	0.0795	0.0939	0.1078	0.1213	0.1345	0.1472	0.1596	0.1716	0.1833	0.1946	0.2057	0.2164	0.2269	0.2371	0.2470	0.0255
72	3.5	0.0298	0.0440	0.0578	0.0713	0.0843	0.0970	0.1094	0.1214	0.1331	0.1444	0.1555	0.1663	0.1769	0.1871	0.1972	0.2069	0.2165	0.2258	0.0255
63	4	0.0270	0.0400	0.0526	0.0649	0.0769	0.0886	0.1000	0.1111	0.1219	0.1325	0.1428	0.1529	0.1627	0.1724	0.1818	0.1910	0.1999	0.2087	0.0255
56	4.5	0.0248	0.0368	0.0484	0.0598	0.0710	0.0818	0.0924	0.1028	0.1129	0.1228	0.1325	0.1420	0.1512	0.1603	0.1692	0.1779	0.1864	0.1947	0.0255
51	5	0.0230	0.0342	0.0451	0.0557	0.0661	0.0763	0.0862	0.0960	0.1055	0.1148	0.1240	0.1329	0.1417	0.1503	0.1588	0.1670	0.1751	0.1831	0.0255
46	5.5	0.0216	0.0320	0.0422	0.0522	0.0620	0.0716	0.0811	0.0903	0.0993	0.1082	0.1168	0.1254	0.1337	0.1419	0.1500	0.1578	0.1656	0.1732	0.0255
42	6	0.0203	0.0302	0.0399	0.0493	0.0586	0.0677	0.0767	0.0854	0.0940	0.1025	0.1108	0.1189	0.1269	0.1347	0.1424	0.1500	0.1574	0.1647	0.0255
39	6.5	0.0193	0.0287	0.0378	0.0469	0.0557	0.0644	0.0729	0.0813	0.0895	0.0976	0.1056	0.1134	0.1210	0.1286	0.1360	0.1432	0.1504	0.1574	0.0255
36	7	0.0184	0.0273	0.0361	0.0447	0.0532	0.0615	0.0697	0.0777	0.0856	0.0934	0.1010	0.1085	0.1159	0.1232	0.1303	0.1373	0.1443	0.1511	0.0255
34	7.5	0.0176	0.0262	0.0346	0.0429	0.0510	0.0590	0.0669	0.0746	0.0822	0.0897	0.0971	0.1043	0.1114	0.1185	0.1254	0.1322	0.1389	0.1455	0.0255
32	8	0.0169	0.0252	0.0333	0.0412	0.0491	0.0568	0.0644	0.0719	0.0792	0.0865	0.0936	0.1006	0.1075	0.1143	0.1210	0.1276	0.1341	0.1405	0.0255
30	8.5	0.0163	0.0243	0.0321	0.0398	0.0474	0.0549	0.0622	0.0694	0.0766	0.0836	0.0905	0.0973	0.1040	0.1106	0.1171	0.1235	0.1299	0.1361	0.0255
28	9	0.0158	0.0235	0.0311	0.0385	0.0459	0.0531	0.0603	0.0673	0.0742	0.0810	0.0877	0.0944	0.1009	0.1073	0.1137	0.1199	0.1261	0.1321	0.0255
27	9.5	0.0153	0.0228	0.0301	0.0374	0.0445	0.0516	0.0585	0.0653	0.0721	0.0787	0.0853	0.0917	0.0981	0.1044	0.1105	0.1166	0.1227	0.1286	0.0255
25	10	0.0149	0.0221	0.0293	0.0364	0.0433	0.0502	0.0569	0.0636	0.0702	0.0766	0.0830	0.0893	0.0956	0.1017	0.1077	0.1137	0.1196	0.1254	0.0255
24	10.5	0.0145	0.0216	0.0286	0.0354	0.0422	0.0489	0.0555	0.0620	0.0684	0.0748	0.0810	0.0872	0.0933	0.0993	0.1052	0.1110	0.1168	0.1225	0.0255
23	11	0.0141	0.0211	0.0279	0.0346	0.0412	0.0478	0.0542	0.0606	0.0669	0.0731	0.0792	0.0852	0.0912	0.0971	0.1029	0.1086	0.1143	0.1199	0.0255
22	11.5	0.0138	0.0206	0.0273	0.0338	0.0403	0.0467	0.0531	0.0593	0.0655	0.0715	0.0775	0.0835	0.0893	0.0951	0.1008	0.1064	0.1120	0.1175	0.0255
21	12	0.0135	0.0202	0.0267	0.0331	0.0395	0.0458	0.0520	0.0581	0.0642	0.0701	0.0760	0.0818	0.0876	0.0933	0.0989	0.1044	0.1099	0.1153	0.0255
20	12.5	0.0133	0.0198	0.0262	0.0325	0.0388	0.0449	0.0510	0.0570	0.0630	0.0688	0.0746	0.0804	0.0860	0.0916	0.0971	0.1025	0.1079	0.1132	0.0255
19	13	0.0130	0.0194	0.0257	0.0319	0.0381	0.0441	0.0501	0.0560	0.0619	0.0677	0.0734	0.0790	0.0845	0.0900	0.0955	0.1008	0.1061	0.1114	0.0255
19	13.5	0.0128	0.0191	0.0253	0.0314	0.0374	0.0434	0.0493	0.0551	0.0609	0.0666	0.0722	0.0777	0.0832	0.0886	0.0940	0.0993	0.1045	0.1097	0.0255
13	20	0.0110	0.0165	0.0219	0.0272	0.0324	0.0376	0.0428	0.0479	0.0529	0.0579	0.0628	0.0677	0.0725	0.0773	0.0820	0.0867	0.0914	0.0959	0.0255

Table 2. Summary of predicted prevalence rates for Ichthophonus for varying levels of median survival time δ and infection rates ϕ. The natural mortality rate for all other causes is assumed to be 0.2 and the fishing mortality rate is assumed to be 0.2.

Median Survival Time (d)	M2	phi=0.01	phi=0.015	phi=0.02	phi=0.025	phi=0.03	phi=0.035	phi=0.04	phi=0.045	phi=0.05	phi=0.055	phi=0.06	phi=0.065	phi=0.07	phi=0.075	phi=0.08	phi=0.085	phi=0.09	phi=0.095	Observed Prevalence 2013
2530	0.1	0.1646	0.2281	0.2826	0.3300	0.3715	0.4081	0.4407	0.4699	0.4962	0.5200	0.5417	0.5615	0.5797	0.5964	0.6118	0.6261	0.6394	0.6518	0.0255
632	0.4	0.1111	0.1579	0.2000	0.2380	0.2727	0.3043	0.3333	0.3599	0.3846	0.4073	0.4285	0.4482	0.4666	0.4838	0.4999	0.5151	0.5293	0.5428	0.0255
361	0.7	0.0844	0.1215	0.1557	0.1874	0.2167	0.2440	0.2695	0.2933	0.3156	0.3366	0.3563	0.3748	0.3923	0.4089	0.4246	0.4395	0.4536	0.4670	0.0255
253	1	0.0685	0.0994	0.1282	0.1553	0.1808	0.2047	0.2273	0.2487	0.2689	0.2880	0.3062	0.3234	0.3398	0.3555	0.3704	0.3847	0.3983	0.4113	0.0255
169	1.5	0.0526	0.0769	0.0999	0.1219	0.1428	0.1627	0.1817	0.1999	0.2173	0.2339	0.2499	0.2652	0.2799	0.2940	0.3076	0.3206	0.3332	0.3453	0.0255
126	2	0.0431	0.0633	0.0826	0.1012	0.1190	0.1361	0.1526	0.1685	0.1838	0.1985	0.2127	0.2264	0.2397	0.2525	0.2648	0.2768	0.2884	0.2996	0.0255
101	2.5	0.0368	0.0541	0.0709	0.0871	0.1027	0.1178	0.1324	0.1466	0.1603	0.1735	0.1863	0.1988	0.2108	0.2225	0.2339	0.2449	0.2557	0.2661	0.0255
84	3	0.0323	0.0476	0.0625	0.0769	0.0909	0.1045	0.1176	0.1304	0.1429	0.1549	0.1667	0.1781	0.1892	0.2000	0.2105	0.2208	0.2308	0.2405	0.0255
72	3.5	0.0289	0.0427	0.0562	0.0692	0.0819	0.0943	0.1063	0.1181	0.1295	0.1406	0.1515	0.1620	0.1724	0.1824	0.1923	0.2018	0.2112	0.2204	0.0255
63	4	0.0263	0.0389	0.0512	0.0632	0.0749	0.0863	0.0974	0.1083	0.1189	0.1293	0.1394	0.1493	0.1589	0.1684	0.1776	0.1866	0.1954	0.2041	0.0255
56	4.5	0.0242	0.0359	0.0473	0.0584	0.0693	0.0799	0.0903	0.1004	0.1103	0.1200	0.1295	0.1388	0.1479	0.1568	0.1656	0.1741	0.1825	0.1907	0.0255
51	5	0.0225	0.0334	0.0440	0.0544	0.0646	0.0746	0.0843	0.0939	0.1032	0.1124	0.1214	0.1302	0.1388	0.1473	0.1556	0.1637	0.1717	0.1795	0.0255
46	5.5	0.0211	0.0313	0.0413	0.0511	0.0607	0.0702	0.0794	0.0884	0.0973	0.1060	0.1145	0.1229	0.1311	0.1392	0.1471	0.1549	0.1625	0.1700	0.0255
42	6	0.0199	0.0296	0.0391	0.0484	0.0575	0.0664	0.0752	0.0838	0.0923	0.1005	0.1087	0.1167	0.1246	0.1323	0.1399	0.1473	0.1546	0.1618	0.0255
39	6.5	0.0189	0.0281	0.0371	0.0460	0.0547	0.0632	0.0716	0.0798	0.0879	0.0959	0.1037	0.1113	0.1189	0.1263	0.1336	0.1408	0.1478	0.1548	0.0255
36	7	0.0180	0.0268	0.0354	0.0439	0.0522	0.0604	0.0685	0.0764	0.0841	0.0918	0.0993	0.1067	0.1140	0.1211	0.1282	0.1351	0.1419	0.1486	0.0255
34	7.5	0.0173	0.0257	0.0340	0.0421	0.0501	0.0580	0.0657	0.0734	0.0808	0.0882	0.0955	0.1026	0.1096	0.1166	0.1234	0.1301	0.1367	0.1432	0.0255
32	8	0.0166	0.0247	0.0327	0.0406	0.0483	0.0559	0.0633	0.0707	0.0779	0.0851	0.0921	0.0990	0.1058	0.1125	0.1191	0.1257	0.1321	0.1384	0.0255
30	8.5	0.0160	0.0239	0.0316	0.0392	0.0466	0.0540	0.0612	0.0683	0.0754	0.0823	0.0891	0.0958	0.1024	0.1089	0.1154	0.1217	0.1280	0.1341	0.0255
28	9	0.0155	0.0231	0.0306	0.0379	0.0452	0.0523	0.0593	0.0663	0.0731	0.0798	0.0864	0.0930	0.0994	0.1057	0.1120	0.1182	0.1243	0.1303	0.0255
27	9.5	0.0151	0.0224	0.0297	0.0368	0.0439	0.0508	0.0576	0.0644	0.0710	0.0776	0.0840	0.0904	0.0967	0.1029	0.1090	0.1150	0.1210	0.1268	0.0255
25	10	0.0146	0.0218	0.0289	0.0358	0.0427	0.0494	0.0561	0.0627	0.0692	0.0756	0.0819	0.0881	0.0942	0.1003	0.1063	0.1121	0.1180	0.1237	0.0255
24	10.5	0.0143	0.0213	0.0281	0.0349	0.0416	0.0482	0.0547	0.0612	0.0675	0.0737	0.0799	0.0860	0.0920	0.0979	0.1038	0.1096	0.1153	0.1209	0.0255
23	11	0.0139	0.0207	0.0275	0.0341	0.0407	0.0471	0.0535	0.0598	0.0660	0.0721	0.0781	0.0841	0.0900	0.0958	0.1015	0.1072	0.1128	0.1183	0.0255
22	11.5	0.0136	0.0203	0.0269	0.0334	0.0398	0.0461	0.0523	0.0585	0.0646	0.0706	0.0765	0.0824	0.0881	0.0938	0.0995	0.1050	0.1105	0.1160	0.0255
21	12	0.0133	0.0199	0.0263	0.0327	0.0390	0.0452	0.0513	0.0574	0.0633	0.0692	0.0750	0.0808	0.0865	0.0921	0.0976	0.1031	0.1085	0.1138	0.0255
20	12.5	0.0131	0.0195	0.0258	0.0321	0.0383	0.0443	0.0504	0.0563	0.0622	0.0680	0.0737	0.0793	0.0849	0.0904	0.0959	0.1013	0.1066	0.1119	0.0255
19	13	0.0128	0.0192	0.0254	0.0315	0.0376	0.0436	0.0495	0.0553	0.0611	0.0668	0.0724	0.0780	0.0835	0.0889	0.0943	0.0996	0.1049	0.1100	0.0255
19	13.5	0.0126	0.0188	0.0250	0.0310	0.0370	0.0429	0.0487	0.0544	0.0601	0.0657	0.0713	0.0768	0.0822	0.0876	0.0929	0.0981	0.1033	0.1084	0.0255
13	20	0.0109	0.0163	0.0216	0.0269	0.0321	0.0372	0.0423	0.0473	0.0523	0.0573	0.0621	0.0670	0.0718	0.0765	0.0812	0.0858	0.0904	0.0950	0.0255

Table 3. Summary of predicted total catch for varying levels of median survival time δ (i.e., M2) and infection rates ϕ. The natural mortality rate for all other causes is assumed to be 0.2 and the fishing mortality rate is assumed to be 0.2.

M2	phi=0.01	phi=0.015	phi=0.02	phi=0.025	phi=0.03	phi=0.035	phi=0.04	phi=0.045	phi=0.05	phi=0.055	phi=0.06	phi=0.065	phi=0.07	phi=0.075	phi=0.08	phi=0.085	phi=0.09	phi=0.095
0.1	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
0.4	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
0.7	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
1	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
1.5	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
2	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
2.5	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
3	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
3.5	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
4	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
4.5	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
5	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
5.5	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
6	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
6.5	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
7	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
7.5	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
8	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
8.5	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
9	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
9.5	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
10	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
10.5	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
11	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
11.5	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
12	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
12.5	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
13	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
13.5	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502
20	0.4016	0.3656	0.3356	0.3101	0.2882	0.2692	0.2525	0.2378	0.2247	0.2130	0.2024	0.1928	0.1841	0.1762	0.1689	0.1622	0.1560	0.1502

Table 4. Summary of predicted ratio of losses due to natural mortality (L(M1)+L(M2)) vs fishing loses (C_T) for varying levels of median survival time δ (i.e., M2) and infection rates ϕ. The natural mortality rate for all other causes is assumed to be 0.2 and the fishing mortality rate is assumed to be 0.2.

M2	phi=0.01	phi=0.015	phi=0.02	phi=0.025	phi=0.03	phi=0.035	phi=0.04	phi=0.045	phi=0.05	phi=0.055	phi=0.06	phi=0.065	phi=0.07	phi=0.075	phi=0.08	phi=0.085	phi=0.09	phi=0.095
0.1	1.2940	1.4411	1.5881	1.7351	1.8821	2.0291	2.1762	2.3232	2.4702	2.6172	2.7642	2.9113	3.0583	3.2053	3.3523	3.4993	3.6464	3.7934
0.4	1.3675	1.5513	1.7351	1.9189	2.1026	2.2864	2.4702	2.6540	2.8377	3.0215	3.2053	3.3891	3.5728	3.7566	3.9404	4.1242	4.3079	4.4917
0.7	1.4010	1.6014	1.8019	2.0024	2.2029	2.4034	2.6039	2.8043	3.0048	3.2053	3.4058	3.6063	3.8067	4.0072	4.2077	4.4082	4.6087	4.8092
1	1.4201	1.6301	1.8401	2.0501	2.2602	2.4702	2.6802	2.8903	3.1003	3.3103	3.5203	3.7304	3.9404	4.1504	4.3605	4.5705	4.7805	4.9905
1.5	1.4385	1.6577	1.8770	2.0962	2.3154	2.5347	2.7539	2.9732	3.1924	3.4116	3.6309	3.8501	4.0694	4.2886	4.5078	4.7271	4.9463	5.1656
2	1.4492	1.6738	1.8985	2.1231	2.3477	2.5723	2.7969	3.0215	3.2461	3.4708	3.6954	3.9200	4.1446	4.3692	4.5938	4.8184	5.0430	5.2677
2.5	1.4563	1.6844	1.9125	2.1407	2.3688	2.5969	2.8251	3.0532	3.2813	3.5095	3.7376	3.9657	4.1939	4.4220	4.6502	4.8783	5.1064	5.3346
3	1.4612	1.6919	1.9225	2.1531	2.3837	2.6143	2.8450	3.0756	3.3062	3.5368	3.7674	3.9981	4.2287	4.4593	4.6899	4.9205	5.1512	5.3818
3.5	1.4649	1.6974	1.9299	2.1623	2.3948	2.6273	2.8597	3.0922	3.3247	3.5571	3.7896	4.0221	4.2545	4.4870	4.7195	4.9519	5.1844	5.4169
4	1.4678	1.7017	1.9356	2.1695	2.4034	2.6373	2.8712	3.1051	3.3390	3.5728	3.8067	4.0406	4.2745	4.5084	4.7423	4.9762	5.2101	5.4440
4.5	1.4701	1.7051	1.9401	2.1752	2.4102	2.6452	2.8803	3.1153	3.3503	3.5854	3.8204	4.0554	4.2904	4.5255	4.7605	4.9955	5.2306	5.4656
5	1.4719	1.7079	1.9438	2.1798	2.4157	2.6517	2.8877	3.1236	3.3596	3.5955	3.8315	4.0675	4.3034	4.5394	4.7753	5.0113	5.2472	5.4832
5.5	1.4735	1.7102	1.9469	2.1836	2.4204	2.6571	2.8938	3.1305	3.3673	3.6040	3.8407	4.0775	4.3142	4.5509	4.7876	5.0244	5.2611	5.4978
6	1.4748	1.7121	1.9495	2.1869	2.4243	2.6616	2.8990	3.1364	3.3738	3.6111	3.8485	4.0859	4.3233	4.5606	4.7980	5.0354	5.2728	5.5101
6.5	1.4759	1.7138	1.9517	2.1897	2.4276	2.6655	2.9034	3.1414	3.3793	3.6172	3.8552	4.0931	4.3310	4.5690	4.8069	5.0448	5.2828	5.5207
7	1.4768	1.7152	1.9536	2.1921	2.4305	2.6689	2.9073	3.1457	3.3841	3.6225	3.8609	4.0993	4.3378	4.5762	4.8146	5.0530	5.2914	5.5298
7.5	1.4777	1.7165	1.9553	2.1941	2.4330	2.6718	2.9106	3.1495	3.3883	3.6271	3.8660	4.1048	4.3436	4.5824	4.8213	5.0601	5.2989	5.5378
8	1.4784	1.7176	1.9568	2.1960	2.4352	2.6744	2.9136	3.1528	3.3920	3.6312	3.8704	4.1096	4.3488	4.5880	4.8272	5.0664	5.3056	5.5448
8.5	1.4791	1.7186	1.9581	2.1976	2.4372	2.6767	2.9162	3.1557	3.3953	3.6348	3.8743	4.1139	4.3534	4.5929	4.8324	5.0720	5.3115	5.5510
9	1.4796	1.7195	1.9593	2.1991	2.4389	2.6787	2.9186	3.1584	3.3982	3.6380	3.8778	4.1177	4.3575	4.5973	4.8371	5.0769	5.3168	5.5566
9.5	1.4802	1.7202	1.9603	2.2004	2.4405	2.6806	2.9207	3.1607	3.4008	3.6409	3.8810	4.1211	4.3612	4.6012	4.8413	5.0814	5.3215	5.5616
10	1.4806	1.7210	1.9613	2.2016	2.4419	2.6822	2.9226	3.1629	3.4032	3.6435	3.8839	4.1242	4.3645	4.6048	4.8451	5.0855	5.3258	5.5661
10.5	1.4811	1.7216	1.9621	2.2027	2.4432	2.6838	2.9243	3.1648	3.4054	3.6459	3.8864	4.1270	4.3675	4.6081	4.8486	5.0891	5.3297	5.5702
11	1.4815	1.7222	1.9629	2.2037	2.4444	2.6851	2.9259	3.1666	3.4073	3.6481	3.8888	4.1295	4.3703	4.6110	4.8518	5.0925	5.3332	5.5740
11.5	1.4818	1.7227	1.9637	2.2046	2.4455	2.6864	2.9273	3.1682	3.4092	3.6501	3.8910	4.1319	4.3728	4.6137	4.8546	5.0956	5.3365	5.5774
12	1.4822	1.7232	1.9643	2.2054	2.4465	2.6876	2.9286	3.1697	3.4108	3.6519	3.8930	4.1341	4.3751	4.6162	4.8573	5.0984	5.3395	5.5805
12.5	1.4825	1.7237	1.9649	2.2062	2.4474	2.6886	2.9299	3.1711	3.4123	3.6536	3.8948	4.1360	4.3773	4.6185	4.8597	5.1010	5.3422	5.5835
13	1.4828	1.7241	1.9655	2.2069	2.4483	2.6896	2.9310	3.1724	3.4138	3.6551	3.8965	4.1379	4.3793	4.6206	4.8620	5.1034	5.3448	5.5861
13.5	1.4830	1.7245	1.9660	2.2075	2.4490	2.6906	2.9321	3.1736	3.4151	3.6566	3.8981	4.1396	4.3811	4.6226	4.8641	5.1056	5.3471	5.5886
20	1.4853	1.7279	1.9705	2.2132	2.4558	2.6984	2.9410	3.1837	3.4263	3.6689	3.9116	4.1542	4.3968	4.6395	4.8821	5.1247	5.3674	5.6100