Approaches for Determining Effects of Pollution on Fish Populations of Puget Sound

JOHN T. LANDAHL, LYNDAL L. JOHNSON, JOHN E. STEIN,
TRACY K. COLLIER, AND USHA VARANASI

*Northwest Fisheries Science Center, National Marine Fisheries Service
2725 Montlake Boulevard East, Seattle, Washington 98112, USA*

Abstract.—Puget Sound is a large marine and estuarine ecosystem in Washington State that serves as the habitat for a number of recreationally and commercially important species of ground-fish and Pacific salmon *Onchorhynchus* spp. Over the past several decades, the human population of the Puget Sound drainage basin has increased substantially, resulting in increased habitat deg-radation and chemical pollution. There is now a body of evidence showing that groundfish and salmon in Puget Sound are experiencing a range of biological effects from chemical contaminant exposure, including impairment of several stages in the reproductive process, increased suscep-tibility to pathogens resulting from altered immune competence, and development of toxicopathic diseases. Preliminary studies suggest the potential for reduced survival of fish from urban areas of Puget Sound resulting from increased infectious and idiopathic diseases. The question that now must be addressed is whether contaminant-related reductions in reproductive and survival rates are sufficient to affect fish abundance in Puget Sound. In the current study, the potential impact of contaminant-related mortality and reproductive impairment on the population growth rate of English sole *Pleuronectes vetulus* was examined by simulation modeling. An initial Leslie matrix population model was constructed for investigation of contaminant effects. The adult mortality rate for English sole in Puget Sound was estimated from recent historical data. Age-specific fecundity was determined from previously collected English sole ovary samples. Existing data on the effects of contaminants on reproduction, including impaired gonadal development, reduced spawning ability, and decreased egg and larval viability, were incorporated into the fecundity component of the model. The influence of density-dependent population regulation on model results was also examined. Results suggest that declines in the fecundity component of the model, like those observed in field studies of fish from contaminated sites such as the Duwamish Waterway and Eagle Harbor, could substantially decrease the population growth rate (r) if density dependence is weak or moderate. Estimated declines in r are comparable in magnitude to those associated with typical levels of commercial fishing pressure. However, a compensation for loss of recruits due to contaminant effects is observed if strong density-dependent population regulation is as-sumed.

Populations of several commercially and re-creationally important species of marine fish, in-cluding English sole *Pleuronectes vetulus*, have se-riously declined since the mid-1980s, either throughout Puget Sound, Washington, or in se-lected embayments in the Puget Sound region (Bargmann 1988; Schmitt et al. 1994). The reasons for these declines are not clear, but potential con-tributing factors include overharvesting, natural changes in environmental or climatic conditions, and various types of habitat degradation, including the discharge of toxic chemicals into the marine environment.

Various studies (e.g., Malins et al. 1984, 1985; Krahn et al. 1986; Varanasi et al. 1989; PSWQA 1992a, 1993; Stein et al. 1992) show that English sole from industrialized areas Puget Sound take up and accumulate or metabolize chemical contami-nants such as aromatic and chlorinated hydrocar-bons. Documented effects of contaminants on En-glish sole in Puget Sound include liver cancer and associated precancerous lesions (Malins et al. 1984, 1985; Krahn et al. 1986; Myers et al. 1990, in press; PSWQA 1992a, 1993) and altered im-mune function (Arkoosh et al. 1996). Liver cancer and other toxicopathic diseases could potentially decrease sole abundance by reducing survival rates, and there is evidence of increased mortality in other fish species as a result of toxicopathic liver disease (Baumann et al. 1990). English soles from contaminated sites also exhibit reproductive im-pairment (Johnson et al. 1988, 1993a; Casillas et al. 1991; Collier et al. 1992). As with disease im-pairments, reproductive alterations could contrib-ute to population declines if their effects were not mitigated by regulatory mechanisms such as den-sity-dependent increases in survival and recruit-ment.

There is little long-term information on English sole abundance in commercially unfished urban

bays, so the effects of chemical contaminants on fish populations in such areas cannot be readily determined from trawl surveys or tagging study data (Schmitt et al. 1994). An alternative approach to addressing the question of impacts of contaminants on the English sole population is to formulate and analyze a mathematical model of that population. While modeling is a less direct approach than field population studies, it has the advantages of being less expensive and permitting investigation of potential population fluctuations over much longer time scales than can feasibly be examined in field studies.

In this study we examine the effects of contaminant exposure on the English sole population in urban and reference bays of central Puget Sound using a deterministic, age-classified Leslie matrix model (Leslie 1945). Analysis of such a model can focus on a number of indices, including long-term population size and the intrinsic rate of natural increase (r), reproductive value or potential, population resilience and risk of population extinction, and sensitivity of the dominant eigenvalue of the matrix to changes in the model parameters (Caswell 1989). Such models have been discussed in detail by Usher (1972) and Caswell (1989), and their use in assessing effects of toxicants on populations of organisms was summarized by Barnthouse (1993). The use of a Leslie matrix model provides a framework for further studies and also allows sensitivity analyses to be performed.

To construct a Leslie matrix model, it is critical to obtain accurate data on age-specific survival and reproductive rates for animals under various exposure conditions. In most previous studies of the impacts of contaminants on fish populations, the effects of single compounds, based on water column toxicity, have been used to estimate survival and reproductive impacts. This method necessitates extrapolation from tested species of fish to untested ones, and data are derived primarily from laboratory toxicity tests (e.g., Barnthouse et al. 1987, 1990; Barnthouse and Van Winkle 1988).

For more realistic model development it is preferable to base estimates of population-level toxicant impacts on data collected for the species of interest. For the present study, a substantial body of data for English sole was available from previous research into the effects of chemical contaminants on survival and reproduction. We based the present model on data on the survival, growth, and reproductive success of English sole, derived from field and laboratory studies conducted in Puget Sound over the past 15 years (Malins et al.

1984, 1985; Johnson et al. 1988; Casillas et al. 1991; Johnson and Landahl 1994). Most of these data pertain to four sites (Port Susan, Sinclair Inlet, Duwamish Waterway, and Eagle Harbor) that have various degrees of sediment contamination (Figure 1). The major sediment-associated contaminants at these sites include polycyclic aromatic hydrocarbons (PAHs), polychlorinated biphenyls (PCBs), and metals. The PAHs and PCBs are more consistently associated with biological effects in fish from marine systems than are the metals (Johnson et al. 1993b; Meador et al. 1994; Myers et al. 1994, in press).

The primary objective of our study was to compare survival rates, reproductive rates, and projected population growth rates of English soles from sites in Puget Sound with different levels of sediment contamination (Landahl and Johnson 1993; Johnson and Landahl 1994). We determined site-specific survival rates from English sole age-frequency data (Johnson and Landahl 1994), while reproductive rates were based on field and laboratory data on English sole gonadal development, fecundity, and spawning success at urban and nonurban sites (Johnson et al. 1988, 1997; Casillas et al. 1991; Collier et al. 1992).

To better assess the magnitude of contaminant-related changes in population growth rates, we also calculated intrinsic population growth rates (r) and net reproductive rates (net R_0) for hypothetical English sole populations with significant mortality due to fishing pressure, but with age-specific reproductive rates equivalent to our estimates for reference animals from nonurban sites. The relative impacts of fishing and contaminants on r and net R_0 were then compared.

The impact of contaminant-associated changes in survival and reproduction of fish abundance will be greatly influenced by the extent to which these anthropogenic alterations can be mitigated by regulatory mechanisms such as immigration or density-related changes in survival and recruitment. For flatfish, density-dependent mortality in the juvenile life stage may be an important means of population regulation. Density-dependent mortality in juvenile plaice Pleuronectes platessa has been observed in the North Sea (Beverton and Iles 1992a, 1992b) and strong evidence of density-dependent mortality during the juvenile stages for sole Solea vulgares (= Solea solea) and plaice was reported by Myers and Cadigan (1993). Accordingly, we have incorporated density-dependent compensation into our model. Based on recent analyses of stock–recruitment curves (Myers et al.
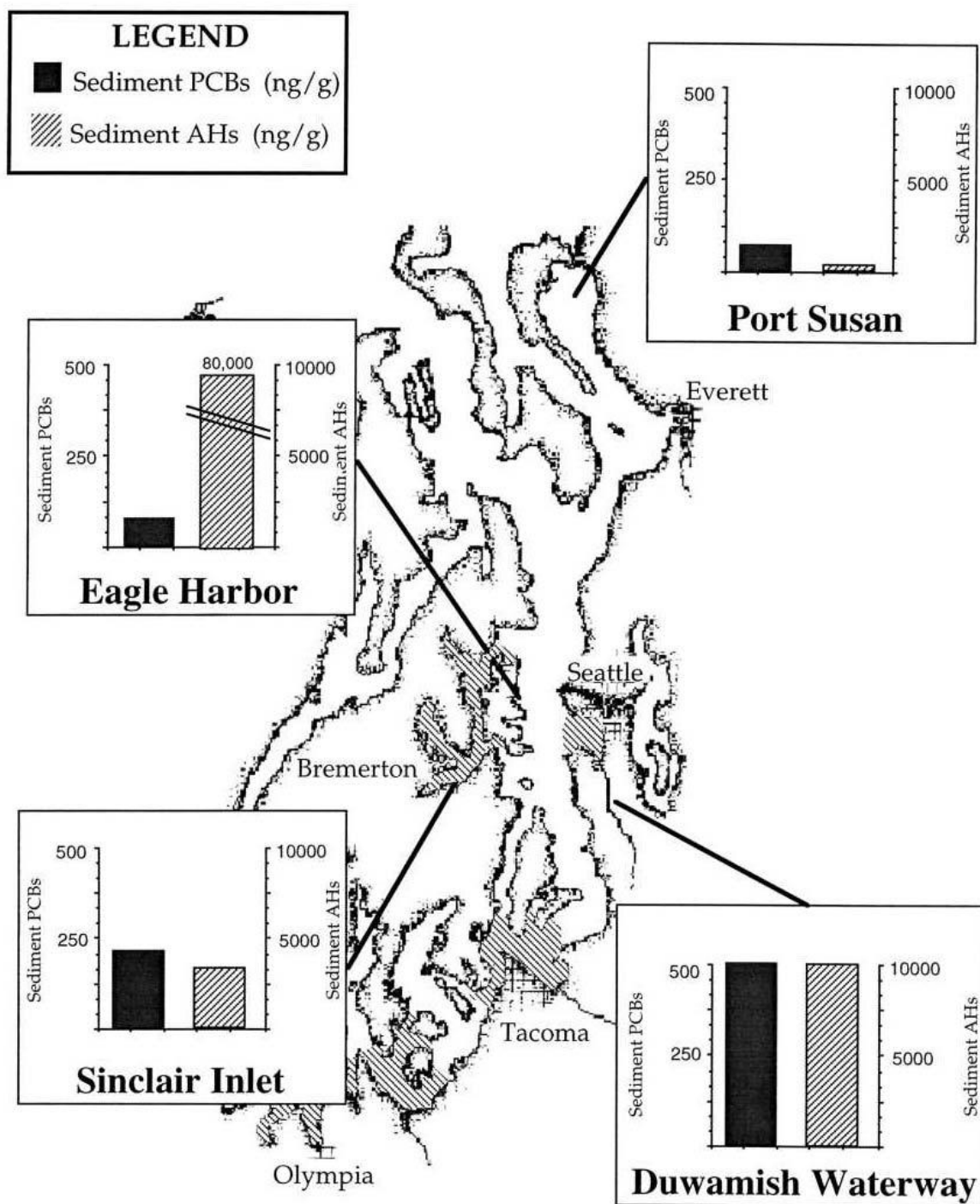
FIGURE 1.—Map of Puget Sound, Washington, showing sites for which data on sediment contamination as well as fecundity and reproductive success estimates for English sole are available (Port Susan, Sinclair Inlet, Duwamish Waterway, and Eagle Harbor). Concentrations (ng/g dry weight) of aromatic hydrocarbons (AHs) and polychlorinated biphenyls (PCBs), the major sediment-associated contaminants at the four study sites (Malins et al. 1984, 1985) are shown in insets. Shaded areas indicate sites where commercial fishing was prohibited in Puget Sound at the time when data used in this model were collected (Bargmann et al. 1985).

1995), there is little evidence for depensation at low population densities in flatfish, so this effect was not considered in the present analysis.

Methods and Sources of Data

Leslie matrix model.—To formulate a Leslie matrix model for English sole, it was necessary to construct a life cycle graph and a life table specifying age-specific mortality (l_x) and age-specific fecundity (m_x) (Caswell 1989). Life table data were obtained from previous English sole toxicology studies conducted in our laboratory and from the published literature as outlined below.

Age-Specific Mortality

Adult survival rate.—Mortality estimates for adult animals were derived from age-frequency data collected for English sole in Puget Sound. Age was estimated by counting opaque zones of whole otoliths—magnified with a dissecting microscope (Chilton and Beamish 1982). Using catch-curve analysis of over 1,000 English soles collected by other trawl in central Puget Sound between 1979 and 1985 (Malins et al. 1980, 1982, 1985), we estimated a total annual survival rate (S) of 0.62 for fish 3 years old and older (Johnson and Landahl 1994). (The trawl was 10.8 m in total length with a 7.5 m opening, 3.8-cm mesh in the body of the net, and an 0.64-cm mesh liner in the cod end.) This rate is very similar to annual survival rates estimated for unfished subpopulations of English sole at sites within central and southern Puget Sound (Holland 1969). The average annual survival rate for adult female soles (ages 3–11) in this survey was 0.67. Published annual survival rate estimates for other flatfish species range from 0.41 to 0.90 (Beverton and Holt 1959; Ketchen and Forrester 1966; Van Cleve and El-Sayed 1969; Lee 1972; Pitt 1973); our estimate is thus comparable to those reported by other researchers. Total survival rates (S) for adult English soles at Port Susan, Sinclair Inlet, the Duwamish Waterway, and Eagle Harbor were also calculated from the same data set according to methods described by Johnson and Landahl (1994; Table 1). With the exception of Eagle Harbor, these site-specific survival rates did not differ significantly $(P \leq 0.05)$ from the survival rate for Puget Sound as a whole. The survival rate estimate for Eagle Harbor was significantly higher than the all-Puget Sound estimate, but it was not as reliable as those for other sites, because the fit of the age-frequency regression line $(r^2 = 0.55)$ was relatively poor in comparison to other sites $(0.70 < r^2 < 0.98)$. Con-

TABLE 1.—Instantaneous mortality rates (Z) and annual survival rates (S) for English sole from selected embayments in Puget Sound. Morality rates were calculated from age frequency data by means of linear regression. (Adapted from Johnson and Landahl 1994).

Site	N	r^2	Z	S
Duwamish Waterway	155	0.86	0.40	0.67
Eagle Harbor	78	0.55	0.22	0.81
Sinclair Inlet	87	0.70	0.40	0.67
Port Susan	59	0.90	0.47	0.62
All Puget Sound	1,188	0.98	0.47	0.62

sequently, the overall Puget Sound survival rate of 0.62 was incorporated into the model for fish age 1 and older at all four sites.

Estimates of age-0 survival.—Field data for estimating posthatching survival rates of age-0 English sole were not available, and preliminary examination had indicated that estimates of adult survival rate were much too high to be biologically realistic for larval and young-of-the-year fish (Landahl and Johnson 1993). Consequently, survival rates for age-0 fish (S_0) were obtained by two methods.

First, survival rates derived from field studies of another flatfish species (Beverton and Iles 1992a) were used in lieu of values for English sole. These investigators constructed a provisional life table for the first year of the life of 0-group plaice, a congener of English sole, on their nursery grounds in the North Sea and adjacent European coastal waters. Based on their life table, a value of 2.50×10^{-5} can be calculated from the change from numbers of fertilized eggs to numbers of age-1 recruits. This figure includes egg mortality and predation loss in the natural environment, which cannot be estimated from our field and laboratory spawning studies. Second, a value for early-age survival was calculated by determining the value for age-0 survival (S_{0E}) that yields an r of 0.0 (population equilibrium; Schaaf et al. 1987) for fish from Port Susan, the minimally contaminated reference site. Because the Leslie matrix used in this study was a modified version of the basic Leslie matrix (see below), S_{0E} was calculated by iterative substitution in the Leslie matrix and calculation of the related eigenvalue rather than by using the method of Schaaf et al. (1987) for calculating S_{0E}.

Age-Specific Fecundity

English soles spawn once each year, beginning approximately as 3-year-olds. Spawning takes

place in winter, with the peak spawning period generally occurring in February or March. Adult fish are territorial (Day 1976), but migrate from their home territories to spawning grounds approximately in late January and return in April (Lassuy 1989; Johnson et al. 1991).

To estimate age-specific fecundity (i.e., the number of eggs produced per female), we used fecundity estimates for 113 females (age range, 3–12 years) collected at Port Susan, Sinclair Inlet, Duwamish Waterway, and Eagle Harbor in 1986 and 1989. Fecundity was estimated by the gravimetric method, as described by Bagenal and Braum (1971). Age was estimated from length by constructing age–length curves for female English soles based on otolith age data collected in earlier studies at the same sites. In this way, potential differences in size at age among our study sites were at least partially accounted for; however, intersite variation in age-specific fecundity could be assessed more accurately by determining otolith ages for the specimens involved, and such analyses will be undertaken in the future.

Fecundity was subsequently adjusted to account for effects of contaminant exposure on reproductive output, based on data from earlier studies involving field and laboratory exposure of English soles (Johnson et al. 1988; Casillas et al. 1991) collected from the four sites used for the fecundity study. The reproductive parameters examined in the studies included gonadal development, ability to spawn, and egg and larval viability. The gonadal development study (Johnson et al. 1988) was designed to assess the percentage of animals from urban and nonurban sites that entered vitellogenesis. Fish for this study were sampled in late fall and early winter, before final oocyte maturation and migration of fish to spawning areas; actively spawning females were not observed or collected at any of the sampling sites. However, in late January and February, catch rates for adult soles at all four sampling sites declined dramatically, presumably as a result of fish migration to spawning areas (Johnson et al. 1991).

It was not possible to track individual English soles from the four sampling sites to their spawning sites and observe their reproductive success on the spawning grounds, so as an alternative, vitellogenic females from Port Susan, Sinclair Inlet, the Duwamish Waterway, and Eagle Harbor were brought into the laboratory and artificially induced to spawn through treatment with a luteinizing hormone-releasing hormone analog (LHRH-A). Their eggs were then fertilized with pooled sperm from

Port Susan males. The results of this study (described in Casillas et al. 1991) were used to estimate spawning success and egg and larval viability for English sole from the four study sites. Using these data, as well as fecundity and mortality estimates, we calculated age-specific reproductive output (R_x, the number of larvae metamorphosing successfully into juveniles) for female soles as

$$R_x = m_x \cdot R_O;$$

m_x = age-specific fecundity (adjusted for a 50:50 sex ratio), and R_O = overall reproductive success (by site). Overall reproductive success is the product of the proportions of vitellogenic females, spawning females, fertilized eggs, and normal larvae.

Application of the Model

Once estimates for fecundity and mortality were obtained, a generalized Leslie matrix model for central Puget Sound was constructed. Lacking reliable survival rate estimates for fish younger than 3 years old, we used the overall Puget Sound survival rate estimates for fish 3 years old and older for the 1- and 2-year-old age-classes because it was the best information available at the time. For age-0 fish, two different mortality rates were used: one based on the work of Beverton and Isles (1992a), and one calculated according to the method of Schaaf et al. (1987). Fecundities were adjusted for a 50:50 sex ratio of English sole. English soles may live longer than 11 years, but our samples included very few individuals older than this age (Johnson and Landahl 1994). For this reason, we used the adult survival rate rather than zero as the last element of the matrix (the 11+ age-class). This modification of the basic Leslie matrix is analogous to that used by Usher (1972) in his analysis of population growth for the blue whale Balenoptera musculus. We then used this generalized model to compare the intrinsic rate of natural increase (r) for English sole populations at the four sites for which reproductive success data were available, modifying the matrix each time to incorporate site-specific reproductive rates.

Sensitivity Analysis

Sensitivity analysis of the model was performed by calculating elasticities for the matrix elements. Elasticities help to standardize the effects of survival and fertility, quantitative estimates of which are very different, by measuring sensitivity on a proportional scale (Kroon et al. 1986). The basic

method involves calculating the dominant eigen-value of the Leslie matrix and the sensitivities of the individual elements. Sensitivity is the partial derivative of the eigenvalue with respect to the value of an element. Elasticity is then calculated as the sensitivity weighted by the element divided by the eigenvalue.

Comparison of Contaminant and Fishing Impacts on r and Net R_0

To better understand the potential magnitude of the effects of contaminants on English sole populations in Puget Sound, we compared the effects of contaminant-related changes in vital rates on the intrinsic population growth rate (r) and the net reproductive rate (net R_0) with the changes in r and net R_0 produced by the level of fishing pressure typically observed for commercially exploited English sole stocks (Ketchen 1947; Holland 1969).

For this analysis, we assumed that fishing mortality did not contribute to the total mortality rate for fish from Port Susan, Eagle Harbor, the Duwamish Wateray, and Sinclair Inlet. This assumption is justified for the Duwamish Waterway, Sinclair Inlet, and Eagle Harbor, because records from the Washington State Department of Fish and Wildlife indicate that commercial trawl fishing at these sites was minimal at the time when the data used in the model were collected. In Sinclair Inlet and the Duwamish Waterway, bottom trawl fishing was prohibited because the areas were industrialized or had heavy ship traffic (Bargmann et al. 1985). At Eagle Harbor, the trawl fishery was not officially closed, but frequent ferry traffic in the area made it unsuitable for commercial fishing (G. G. Bargmann, Washington Department of Fish and Wildlife, personal communication). Throughout the late 1970s and 1980s, when much of the data used in this model were collected, there was a significant bottom trawl fishery for English sole in some parts of northern Puget Sound (Bargmann et al. 1985; Schmitt et al. 1991; Figure 1), so it is possible that English sole populations at Port Susan experienced some fishing pressure. However, the similarity of the our mortality rate estimates for sole from this site to estimates of natural mortality at other nonurban sites within Puget Sound (Holland 1969) suggests that the contribution of fishing to mortality was probably fairly minor. We could not take recreational fishing mortality into account due to lack of data; however, records suggest that the majority of English sole harvest is commercial (Schmitt et al. 1994). Estimates of typical levels of fishing mortality for commercially

exploited sole populations were obtained from Ketchen (1947) and Holland (1969). According to these sources, total annual mortality rates (including fishing mortality) ranged from 50 to 67% in the more heavily exploited fishing grounds in the Straits of Georgia, British Columbia, Canada.

We used these data, as well as data on reproductive rates from our Puget Sound reference site, Port Susan, to construct life tables for hypothetical commercially exploited English sole subpopulations. Survival rates for age-classes 0–2 were the same as those used in life tables for Port Susan, the Duwamish Watersay, Sinclair Inlet, and Eagle Harbor. However, for adult soles age 3 and older, annual survival rates of 0.50 and 0.35 were used to reflect the increased mortality due to fishing comparable to that reported by Ketchen (1947) and Holland (1969) in exploited British Columbia English sole stocks. We then calculated r and net R_0 for these hypothetical populations using the RAMAS/Age software package (Ferson et al. 1992).

The intrinsic rate of population growth, r, was calculated as described above. The net reproductive rate was calculated with the formula (Ferson et al. 1992)

$$\text{net } R_0 = l_x f R_x;$$

l_x = longevity (computed as $S_0 \cdot S_1 \cdot S_2 \cdot \ldots \cdot S_{x-1}$, where S_x is the age-specific survival),

f = the sex ratio (assumed to be 50:50), and

R_x = age-specific reproductive output, as defined above.

If net R_0 is larger than one, population abundance is increasing; if it is smaller than one, population abundance is decreasing.

Estimated values for r and net R_0 were then compared to determine if the reductions in these metrics associated with contaminant-related changes in reproductive rates were comparable to those associated with commercial fishing pressure.

Density Dependence

Until recently, density dependence has seldom been addressed with age-structured models such as Leslie matrix models (Caswell 1989). De-Angelis et al. (1980) formulated a Leslie matrix fishery model in which density-dependent compensation occurred only in the first age-class. The basic technique is to add a coefficient to the first two terms in the first row of the matrix. A similar

TABLE 2.—Preliminary summary of fecundity study results for five Puget Sound sites for 1986 and 1989. Average fecundity at each site prior to adjustment for contaminant exposure is given for the two age groups (5 and 6 years old) that were collected at all sites (from Landahl and Johnson 1993).

| | Site | | | | |
Variable	Port Susan	Yukon Harbor	Sinclair Inlet	Duwamish Waterway	Eagle Harbor
Number of females	29	11	19	27	33
Minimum age (year)	3	4	5	4	3
Maximum age (year)	7	6	12	10	8
Average fecundity at age 5	422×10^3	382×10^3	485×10^3	446×10^3	442×10^3
Average fecundity at age 6	562×10^3	488×10^3	667×10^3	813×10^3	575×10^3

approach was advocated by Charnov (1993). This method assumes no effect of adult density on age-specific fecundity. The result of applying this method is that r depends on the population size at the beginning of each time period and will usually change from year to year during a model run.

We incorporated density dependence into our model using the RAMAS/Age software. For this purpose, we used the Beverton–Holt function (Beverton and Holt 1957), since it was originally derived for plaice. This function describes the relationship between reproductive effort and reproductive success. In our study, reproductive effort is defined as the number of female eggs produced, and reproductive success is defined as the number of 0 age-class individuals entering the population (i.e., hatching as viable larvae). The value of r for the Beverton–Holt function in our model was chosen to be that which produces a stable age distribution for Port Susan fish (i.e., 3.8×10^{-11}), and the value of k is for striped bass (5.0×10^{-1}), another marine fish species with high fecundity (Goodyear 1984). These parameters yield a parental investment–recruitment curve of the form typically associated with moderate density dependence (Ferson et al. 1992).

Results

Age-Specific Fecundity

Egg production.—Detailed information on English sole fecundity in Puget Sound is reported in Johnson et al. (1997); these data, prior to adjustment for effects of contaminant exposure on reproductive success, are summarized in Table 2. Young females produced about 300,000 eggs in their first year of reproductive activity (about age 3). The oldest and largest females collected produced over 2 million eggs per year. Age-specific fecundity tended to be higher in English soles from the Duwamish Waterway and Sinclair Inlet sole than in sole from the other two sites. However, the mag-

nitude of the effect was relatively small, accounting for only about 3–4% of the variation in egg production (Johnson et al. 1997). Moreover, the increase in egg production appeared to be associated with a decrease in egg weight. Studies with other flatfish species suggest that such a decline in egg weight could potentially reduce larval survival rates (Buckley et al. 1991), and thus offset the advantage of increased egg production. Additionally, there was considerable uncertainty in the estimates of site-specific age-specific fecundity because of the small data set available, especially for older fish. Consequently, for construction of the present model, we used overall age-specific fecundity for all specimens collected prior to adjustment for effects of contaminant exposure on reproductive success, rather than site-specific fecundity.

Reproductive success.—In addition to information on egg size and egg production, our earlier field and laboratory studies provided data on several aspects of reproductive success, specifically gonadal development, spawning, fertilization success of eggs, and percent normal larvae at all four sites. These studies found that each of these aspects of reproduction were impaired in fish from the contaminated sites. Results of the reproductive success studies are summarized in Table 3. This summary is based on data for the years 1986, 1987, and 1988 reported by Johnson et al. (1988) and Casillas et al. (1991). We also have some evidence suggesting that soles from contaminated sites may be less likely to migrate to spawning grounds (Collier et al. 1992), but because this impact could not be quantified it was not incorporated into the present model.

Reproductive impairment was most notable at the Duwamish Waterway, a site with high concentrations of contaminants in sediment, including PAHs and PCBs, and at Eagle Harbor, a site with very high concentrations of PAHs. At each site,

TABLE 3.—Summary of reproductive success study results for four Puget Sound sites (from Landahl and Johnson 1993). Vitellogenic females are those undergoing gonadal recrudescence and egg development. Sample sizes are in parentheses. Overall reproductive success is the product of the proportions of vitellogenic females, spawning females, fertilized eggs, and normal larvae.

| Reproductive effect | Site | | | |
	Port Susan	Sinclair Inlet	Duwamish Waterway	Eagle Harbor
Vitellogenic females (%)[a]	80 (50)	90 (96)	63 (101)	57 (97)
Females spawning (%)[b]	90 (60)	75 (23)	54 (53)	35 (21)
Eggs fertilized (%)[b]	52 (54)	35 (17)	44 (24)	24 (7)
Normal larvae (%)[b]	74 (53)	54 (14)	59 (20)	68 (4)
Overall reproductive success (%)	28	13	9	3

[a] From Johnson et al. (1988). 1987 data are given for Port Susan and the weighted average of 1986 and 1987 values is given for other sites.
[b] From Casillas et al. (1991). 1988 data are given for Sinclair Inlet and Eagle Harbor, and weighted averages of 1987 and 1988 values are given for Port Susan and Duwamish.

the percentage of adult female English soles entering vitellogenesis was smaller than at Port Susan, which has little sediment contamination (Johnson et al. 1988). Soles from the two polluted sites (Eagle Harbor and the Duwamish Waterway) were also less likely to spawn in response to LHRH-a treatment than soles from Port Susan, and their eggs were less likely to be fertilized. Those eggs which were fertilized were less likely to develop into normal larvae (Casillas et al. 1991).

Based on the estimates of ovarian recrudescence, spawning, fertilization, and larval development, overall reproductive success was 28% for Port Susan, 13% for Sinclair Inlet, 9% for the Duwamish Waterway, and only 3% for Eagle Harbor (Table 3). These estimates of overall reproductive success are more accurate for Port Susan and the Duwamish Waterway than for the other two sites because they are based on 2 years of data rather than 1 (Casillas et al. 1991).

Population Trajectories

The estimates for fecundity and mortality were used to construct a generalized Leslie matrix model, which was then used to compare the intrinsic rate of natural increase (r) for English sole populations at the four sites for which reproductive success data were available. For age-0 fish, two different survival rates were used; one rate was based on Beverton and Isles[1] (1992a) estimate for age-0 survival for plaice and another (S_{OE}) was calculated according to the method of Schaaf et al. (1987; see Methods). When the value for plaice

TABLE 4.—Summary of model results for four Puget Sound sites with progressively increasing levels of sediment PAH contamination with two estimates of larval and early juvenile survival (S_0). Values are the instantaneous rate of population increase (r). The plaice survival estimate is from Beverton and Iles (1992b). The second estimate (1.44 × 10 [5]) was obtained by adjusting the juvenile survival to produce a stable population trajectory for the reference site, Port Susan (Schaaf et al. 1987).

| S_0 | Site | | | |
	Port Susan	Sinclair Inlet	Duwamish Waterway	Eagle Harbor
2.50 × 10⁻⁵ (plaice)	0.08	−0.03	−0.08	−0.21
1.44 × 10⁻⁵ (S_{OE})	0.00	−0.10	−0.15	−0.26

(2.5×10^{-5}) was used, r was 0.08 for Port Susan, −0.03 for Sinclair Inlet, −0.08 for the Duwamish Waterway, and −0.21 for Eagle Harbor (Table 4). The method of Schaaf et al. yielded a value of 1.44 × 10⁻⁵ for S_{OE}. When S_{OE} was used as the estimate for age-0 survival in the Leslie matrix model, r was −0.10 for Sinclair Inlet, −0.15 for the Duwamish Waterway, and −0.26 for Eagle Harbor (Table 4). Values of r decreased with increasing sediment PAH contamination. This difference in r values results in a pronounced divergence of the projected population trajectories over a period of 10 years for fish from Port Susan compared to fish from contaminated sites (Figure 2).

Model Sensitivity

Computation of elasticities for each element of the Leslie matrix (Caswell 1989) indicates that the dominant eigenvalue (and hence the estimate for r) is particularly sensitive to the accuracy of the estimates of survival for age-0 to age-3 fish and to the estimate for age-3 fecundity adjusted for overall reproductive success (Table 5).

Comparison of Fishing and Contaminant Impacts

Estimates of the intrinsic rate of population growth (r) and net reproductive output (net R_0) for English sole subpopulations from Port Susan, Sinclair Inlet, the Duwamish Waterway, and Eagle Harbor are compared in Figure 3 to values of r and net R_0 estimated for hypothetical commercially exploited populations. The reduction in r due to contaminant-associated reproductive impairment at the Duwamish Waterway and Eagle Harbor was comparable to or greater than the reduction in r due to fishing mortality at levels typical of exploited English sole populations from British Columbia (Figure 3A). The same was true
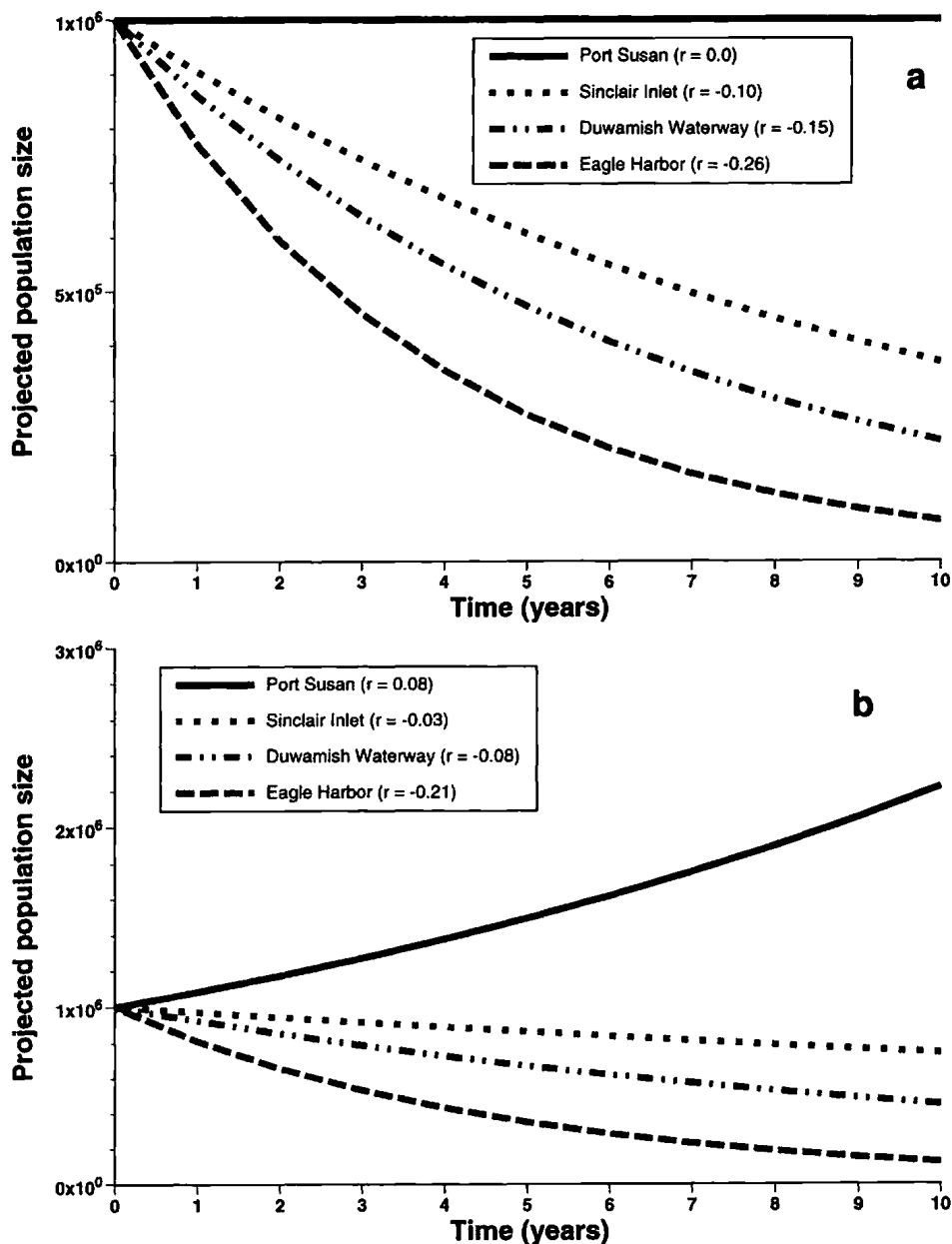
FIGURE 2.—Projected population trajectories over a 10-year period for English sole at four sites in Puget Sound on the basis of r computed from the initial Leslie matrix model with (A) S_{0E} and (B) S_0 for plaice as estimates of age-0 survival. Initial population size is one million.

for estimates of net reproductive output (Figure 3B).

Density Dependence

Projected population trajectories from the modified Leslie matrix model incorporating moderate density dependence are shown in Figure 4A. For ease of comparison, projected population trajectories for Eagle Harbor with and without density

dependence are shown in Figure 4B. These curves are quite similar, but the projected population size at Eagle Harbor remains larger with moderate density dependence than without. Results for the other three sites are qualitatively similar.

It should also be noted that the population trajectory with moderate density dependence is displaced to the right by 1 year. The displacement of the second curve occurs because the RAMAS/Age

TABLE 5.—Elasticity values for parameters with elasticity ≥ 0.10 for three Leslie matrix models, with different estimates of age-0 survival (S_0), indicating that the dominant eigenvalue of the Leslie matrix (and hence the estimate of r) is particularly sensitive to the accuracy of these estimates. Reproductive success is that for Port Susan (0.28) for each model.

	S_0	
	---	---
Parameter	2.50×10^{-5} (plaice)	1.44×10^{-5} (S_{0E})
Age-0 survival	0.16	0.14
Age-1 survival	0.16	0.14
Age-2 survival	0.11	0.14
Age-3 survival	<0.10	0.11
Age-3 fecundity	<0.10	<0.10

model imposes density-dependent mortality after calculating reproductive output, resulting in a time lag before the numbers of age-1 fish are affected by a change in reproductive output.

The expected long-term effect of density dependence is to compensate for contaminant effects. However, the model results suggest that moderate density-dependent regulation does not completely compensate for declines in population growth rate associated with declines in the fecundity component of the model, as observed in field studies in fish from the Duwamish Waterway and Eagle Harbor.

Discussion

Our initial model projections indicate that contaminant effects, particularly in relation to reproductive capacity, could substantially reduce the intrinsic rate of increase (r of English sole populations from contaminated sites in Puget Sound, Washington. Estimated reductions in r were comparable to reductions in r associated with a fishing mortality rates of 15–30%, which are typical of commercially exploited English sole stocks in British Columbia (Ketchen 1947; Holland 1969). This suggests that contaminant impacts are of sufficient magnitude to be a cause for concern, especially if fish inhabiting contaminated estuaries or embayments such as the Duwamish Waterway or Eagle Harbor have historically contributed a significant proportion of recruits to the English sole population of Puget Sound. These findings warrant further research on alternate modeling approaches (e.g., spatially explicit or individual-based models) to increase the biological realism of the model and account for potential compensatory mechanisms more quantitatively.

Geographically, contaminant "hot spots" constitute a relatively small percentage of the sea floor of Puget Sound, and hence on this basis would not appear to be a major influence on the English sole population. However, the relatively narrow band of water 20–60 m in depth nearshore, where contaminant "hot spots" generally occur (PSWQA 1987, 1992b) is an important component of the habitat for both adult and juvenile English soles (Lassuy 1989; Toole et al. 1987), and this area may suffer increasing degradation as the human population in the Puget Sound basin continues to increase. The relationships among total bottom area, bottom area suitable for English sole habitat, and contaminated bottom area constitute a subject for future investigation, as presently we have only qualitative estimates of the proportion of the total Puget Sound sole population that resides at urban sites and so could be susceptible to contaminant-associated declines in survival or reproductive rates. A more quantitative assessment could be made by using data from reproductive surveys in Puget Sound to estimate the threshold sediment concentrations of contaminants, such as PAHs and PCBs, at which decreased reproductive success is first observed. Such an approach would provide an estimate of the geographic area over which animals are at risk. This approach is currently being used successfully with data on toxicopathic lesion prevalences (Johnson et al. 1994; Horness et al., in press) and will be applied to reproductive toxicology data when sufficient information is available.

In contrast to reproductive rates, total mortality rates for English soles from heavily contaminated sites were generally the same or slightly lower than those for soles from the Port Susan reference site and for Puget Sound as a whole (Johnson and Landahl 1994), and the rates were very similar overall to survival and mortality rates calculated by Holland (1969) for subpopulations of English sole from relatively unurbanized sites in central and southern Puget Sound where there was little fishing pressure. Thus, they did not substantially affect the intrinsic growth rate (r) of sole subpopulations from contaminated sites. These findings suggest that although toxicant-related death due to disease or other impairment is likely to contribute to mortality rates in English sole, its impact on adult animals may be overridden by other factors that affect English sole survival. However, additional data are needed to substantiate this preliminary conclusion. For example, more information is needed on historical levels of commercial fishing pressure at nonurban sites in various parts of Puget
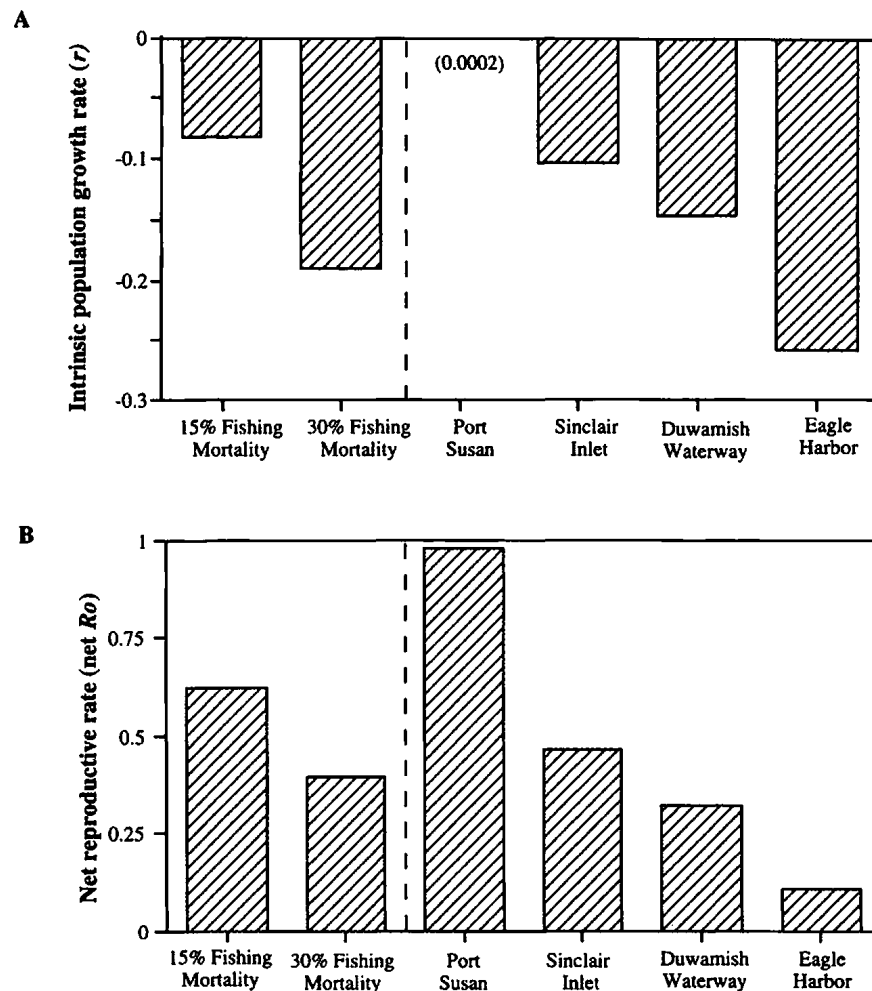
FIGURE 3.—Estimated values of (A) intrinsic rate of population increase (r) and (B) net reproductive rate (R_0) for English sole from Port Susan, Sinclair Inlet, the Duwamish Waterway, and Eagle Harbor, and for hypothetical sole sub-populations with age-specific reproductive rates identical to those estimated for Port Susan reference fish, but increased mortality on adult (age-3+) fish due to fishing pressure. Total mortality rates for the hypothetical populations are 50% and 67%, the same as those estimated for commercially exploited English sole populations in British Columbia waters (Ketchen 1947; Holland 1969).

Sound, particularly in northern part where there has been an active commercial trawl fishery in the past (Menasveta 1958; Holland 1969; Bargmann et al. 1985); information is also needed on all levels of recreational fishing at both urban and non-urban sites. If, for example, levels of recreational fishing are higher in urban than nonurban areas, but total mortality rates are similar at all sites, mortality due to factors other than fishing may actually be somewhat higher in urban than non-urban areas. Additional data are also needed to provide more accurate age-specific mortality rates, especially for older age-classes, which are most likely to be affected by contaminant-associated disease. Because of our limited sample size, rel-

atively small but significant changes in mortality may have been undetectable in our data set. Future work will also need to assess more directly the impacts of contaminants on survival of sole through techniques such as long-term holding studies and disease-challenge experiments.

Our preliminary analyses suggest that density-dependent population regulation mechanisms could partially compensate for contaminant impacts on English sole reproductive and survival rates. However, more accurate information on the strength and extent of density-dependent population regulation mechanisms in English sole is needed to confirm these preliminary findings. Although we have incorporated density dependence
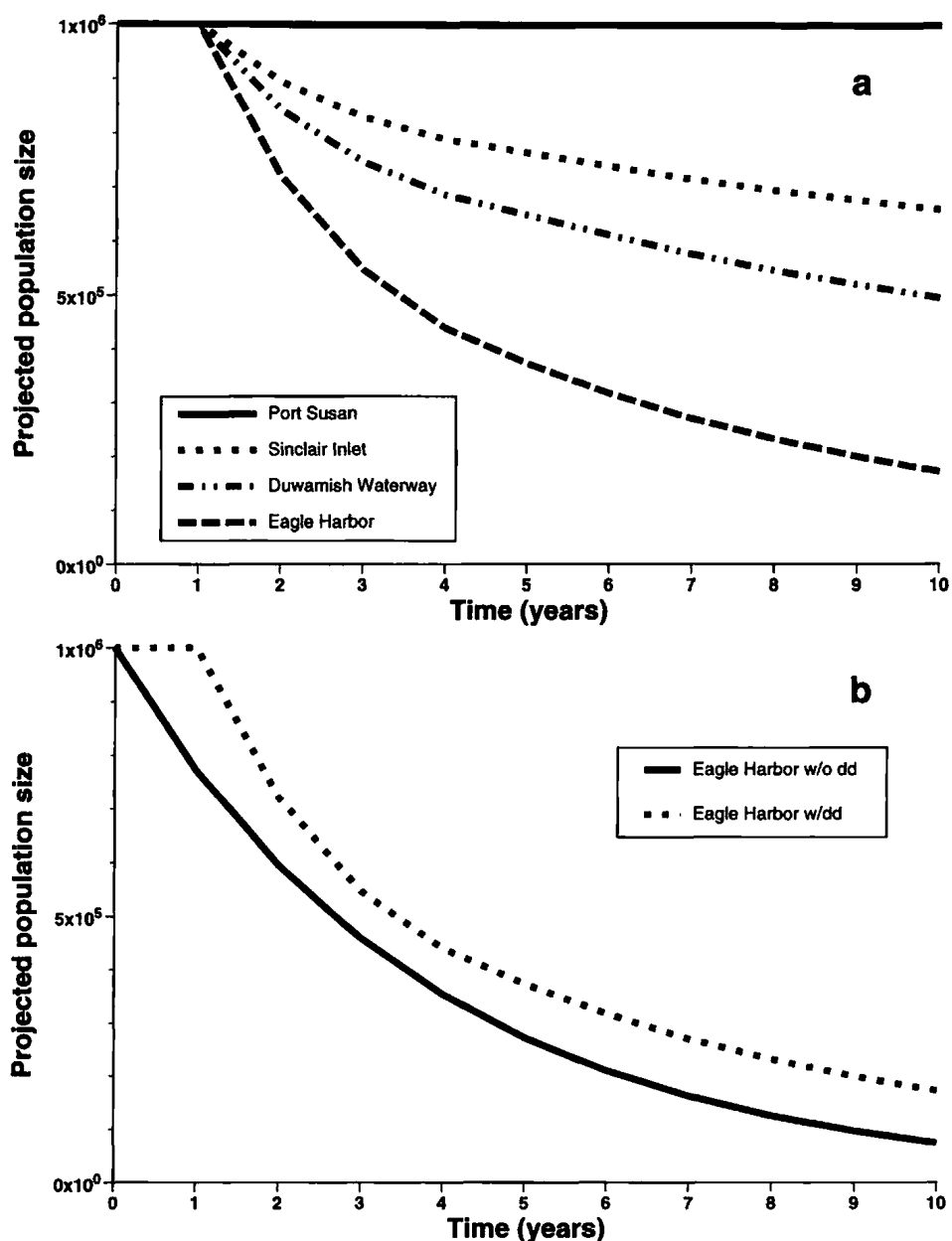
FIGURE 4.—(A) Projected population trajectories over a period of 10 years for English sole at four sites in Puget Sound on the basis of r computed from the modified Leslie matrix model incorporating moderate density dependence. Initial population size is one million. (B) Comparison of projected population trajectories over a period of 10 years for English sole at Eagle Harbor (EH) on the basis of r computed from the initial Leslie matrix model using S_{OE} without density dependence (w/dd) and the modified model incorporating moderate density dependence (w/dd). Initial population size is 1 million.

into our model, we are aware that many marine species have open populations in which there is not a strong coupling between adult population size and subsequent recruitment of juveniles to the population (Hanski and Gilpin 1991; Gaines and Lafferty 1995). Moreover, predation and habitat disturbance may keep all life history stages of the

English sole population of Puget Sound below carrying capacity, so density-dependent mechanisms of population regulation would not come into play.

While our initial model provides insight into the potential effects of chemical contaminants on English sole populations, several refinements are needed to increase the model's ecological rele-

vance. Better estimates of age-0 to age-3 survival obtained from field and laboratory studies with larval and juvenile English soles are critical, because the model is especially sensitive to these parameters; improved data are also needed on both fishing and natural mortality for Puget Sound English sole. The model could also be strengthed by a more careful analysis of site-specific growth rate and age at first sexual maturation, which would provide more accurate data on age-specific fecundity for fish from the four sampling sites. Perhaps most critical, however, is the need to consider the contribution of recruits from urban sites to the central Puget Sound English sole population, as well as the possibility that immigration into contaminated areas by offspring of fish from other sites could compensate for recruitment declines associated with contaminant exposure in localized areas. Without such information, the potential magnitude of pollution impacts on English sole abundance in central Puget Sound cannot be accurately assessed.

Our current modeling approach assumes that local recruitment depends primarily on the reproductive rates of adults residing at the site. However, the life history of English sole is more complex. Adult English sole tend to remain in the same area for long periods (Day 1976), but their spawning sites are distinct from their normal sites of residence and may draw animals from throughout Puget Sound. Moreover, English sole have planktonic eggs and larvae that remain in the water column for up to 10 weeks (Alderice and Forrester 1968; Orsi 1968). Larvae then settle and undergo metamorphosis in nearshore nursery areas, after which they migrate to residential sites that will be their home territories during adult life. Because Puget Sound has strong tides and currents, it is likely that the English sole of Puget Sound constitute a panmictic population, with at least some movement of eggs and larvae from nonurban to urban areas (Ketchen 1956; Laroche and Richardson 1979; Laroche et al. 1982; Lassuy 1989). Juvenile sole might also immigrate from nursery sites in undisturbed areas to contaminated sites. However, the mechanisms regulating the transport of English sole larvae into nursery grounds are poorly understood, and recruitment patterns of juveniles from nursery to adult residential areas within Puget Sound are not well characterized (Toole et al. 1987; Lassuy 1989).

Currently it would be speculative to estimate the extent to which increased recruitment from nonurban areas could compensate for decreased re-

productive output by sole subpopulations from contaminated sites such as Eagle Harbor and the Duwamish Waterway. Metapopulation analyses would be useful; however, there is a need for better field data on actual recruitment and migration patterns in English sole to develop a metapopulation model that would accurately reflect the population biology of this species. We are also in the process of developing a stage-based rather than age-based model to more effectively simulate the distinctive processes affecting the larval, juvenile, and adult life stages of English sole. Development of an individual-based model (DeAngelis and Gross 1992) incorporating aspects of the physiology of English sole and site- or exposure-related differences in reproduction and survival is alternative approach for better assessing the impacts of anthropogenic stressors on the Puget Sound English sole population. Ultimately, the best test of the tentative conclusions drawn from analysis of the initial model would be provided by detailed stock assessment and ongoing monitoring of English sole in this region.

A final consideration is the applicability of the present findings to effective management of marine fish stocks. The value of any approach to assessing population-level impacts from anthropogenic stressors will be of increased value if the information can be incorporated into existing stock assessment models. Effects of contaminants on fecundity, as presented here, when viewed as a form of "population stress," can be expressed in terms related to spawning per recruit, making it possible to use techniques for stock assessment to estimate the decrease in commercial and recreational fishing that would be needed to offset the stress from pollution (Sissenwine and Sheperd 1987; Fogarty et al. 1991). For example, a spawner-recruit model (Hilborn and Walters 1992) can be used to express contaminant effects and fishing pressure in a common currency. If spawning per recruit is decreased by chemical contaminants, the average survival rate of prerecruits (fish from age-0 to age of entry into the spawning population, age-3 in this case) must increase proportionately if stock size is not to decline (M. P. Sissenwine, National Marine Fisheries Service, personal communication). Using a common currency has the clear advantage of allowing an assessment of both the relative and cumulative contributions of multiple stressors (fishing, loss of habitat, and chemical substances) to declines in commercially and recreationally important fisheries, and thereby contributes to improved assessment and management of fisheries

resources by identifying the major stresses on a population.

Conclusion

The population projections presented here, based on field and laboratory data on mortality and fecundity in English sole subpopulations in Puget Sound, suggest the potential for chemical contaminant effects on the intrinsic rate of increase in English sole populations. As is often the case with marine fish, the lack of quantitative data in several areas limited the ability to estimate actual population level impacts. However, techniques such as sensitivity analysis allowed us to identify critical data gaps that must be addressed to increase the confidence in estimating population level impacts from chemical contaminants on English sole from central Puget Sound. Our studies with English sole substantiate that through multidisciplinary studies that combine field and laboratory experiments with quantitative modeling techniques, substantive progress can be made to distinguish quantitatively the effect of chemical pollution on fish stocks. Although chemical contaminants are unlikely to have a predominant influence on offshore fisheries, these substances may have a substantially greater impact in nearshore coastal areas, and the effective regulation of pollution and related anthropogenic impacts may be a key factor in the maintenance of healthy fish stocks in such environments.

Acknowledgments

References

Alderice, D. F., and C. R. Forrester. 1968. Some effects of salinity and temperature on early development and survival of English sole (*Parophrys vetulus*). Journal of the Fisheries Research Board of Canada 25:495–521.

Arkoosh, M. A., and five coauthors. 1996. Leukoproliferative response of splenic leukocytes from English sole (*Pleuronectes vetulus*) exposed to chemical contaminants. Environmental Toxicology and Chemistry 15:1154–1162.

Bagenal, T. B., and E. Braum. 1971. Eggs and early life history. IBP (International Biological Programme) Handbook 3:166–198.

Bargmann, G. G. 1988. Trends in the abundance of economically important marine fish in Puget Sound. Pages 72–75 *in* Proceedings of the First Annual Meeting on Puget Sound Research, volume 1. Puget Sound Water Quality Authority, Seattle.

Bargmann, G. G., M. Pedersen, and R. J. Trumble. 1985. Final environmental impact statement for the continued harvest of bottomfish in Puget Sound by commercial otter trawl gears. Washington Department of Fisheries, Olympia.

Barnthouse, L. W. 1993. Population-level effects. Pages 247–274 *in* G. W. Suter II, editor. Ecological risk assessment. Lewis Publishers, Boca Raton, Florida.

Barnthouse, L. W., G. W. Suter II, and A. E. Rosen. 1990. Risks of toxic contaminants to exploited fish populations: influence of life history, data uncertainty and exploitation intensity. Environmental Toxicology and Chemistry 9:297–311.

Barnthouse, L. W., I. G. W. Suter, A. E. Rosen, and J. J. Beauchamp. 1987. Estimating responses of fish populations to toxic contaminants. Environmental Toxicology and Chemistry 6:811–824.

Barnthouse, L. W., and W. Van Winkle. 1988. Analysis of impingement impacts on Hudson River fish populations. Pages 182–190 *in* L. W. Barnthouse, R. J. Klauda, D. S. Vaugha and R. L. Kendall, editors. Science, law, and Hudson River Power Plants: a case study of environmental impact assessment. American Fisheries Society, Monograph 4, Bethesda, Maryland.

Baumann, P. C., J. C. Harshbarger, and K. J. Hartmann. 1990. Relationship between liver tumors and age in brown bullhead populations from two Lake Erie tributaries. Science of the Total Environment, 94:71–87.

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Fishery Investigations, Series II, Marine Fisheries, Great Britain Ministry of Agriculture Fisheries and Food 19.

Beverton, R. J. H., and S. J. Holt. 1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. Pages 142–180 *in* G. E. W. Wolstenholme and M. O'Conner, editors. Ciba Foundation Colloquia on Aging. V. The lifespan of animals. Churchill, London.

Beverton, R. J. H., and T. C. Iles. 1992a. Mortality rates of 0-group plaice (*Pleuronetes platessa* L.), dab (*Limanda limanda* L.) and turbot (*Scopthalmus maximus* L.) in European waters. II. Comparison of mortality rates and construction of life table for 0-group plaice. Netherlands Journal of Sea Research 29:49–59.

Beverton, R. J. H., and T. C. Iles. 1992b. Mortality rates of 0-group plaice (*Pleuronetes platessa* L.), dab (*Limanda limanda* L.) and turbot (*Scopthalmus maximus* L.) in European waters. III. Density-dependence of mortality rate in 0-group plaice and some demographic implications. Netherlands Journal of Sea Research 29:61–79.

Buckley, L. J., and five coauthors. 1991. Winter flounder *Pseudopleuronectes americanus* reproductive

success. II. Effect of spawning time and female size on size, composition, and viability of eggs and larvae. Marine Ecology Progress Series 74:125–135.

Casillas, E., and seven coauthors. 1991. Inducibility of spawning and reproductive success of female English sole (*Parophrys vetulus*) from urban and non-urban areas of Puget Sound, Washington. Marine Environmental Research 31:99–122.

Caswell, H. 1989. Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Sunderland, Massachusetts.

Charnov, E. L. 1993. Life history invariants: some explorations of symmetry in evolutionary ecology. Oxford University Press, Oxford, UK.

Chilton, D. E., and R. J. Beamish. 1982. Age determination methods for fish studies by the groundfish program at the Pacific Biological Station. Canadian Special Publication of Fisheries and Aquatic Sciences 60:1–54.

Collier, T. K., and five coauthors. 1992. Field studies of reproductive success in English sole (*Parophrys vetulus*): correlations with bioindicators of maternal contaminant exposure. Science of the Total Environment 116:169–185.

Day, D. E. 1976. Homing behavior and population stratification in central Puget Sound English sole (*Parophrys vetulus*). Journal of the Fisheries Research Board of Canada 33:287–292.

DeAngelis, D. L., L. J. Svoboda, S. W. Christensen, and D. S. Vaughn. 1980. Stability and return times of Leslie matrices with density-dependent survival: applications to fish populations. Ecological Modelling 8:149–163.

DeAngelis, D. L., and L. Gross. 1992. Individual-based models in ecology: concepts and models. Chapman and Hall, New York.

Ferson, S., H. R. Akcakaya, and P. D. Fernhout. 1992. Modeling fluctuations in age-structured populations. Applied Biomathematics, Setauket, New York.

Forgarty, M. J., M. P. Sissenwine, and E. B. Cohen. 1991. Recruitment variability and the dynamics of exploited marine populations. Trends in Ecology and Evolution 6:241–246.

Gaines, S. D., and K. D. Lafferty. 1995. Modeling the dynamics of marine species: the importance of incorporating larval dispersal. Pages 389–412 in L. Mc Edward, editor. Ecology of marine invertebrate larvae. CRC Press, New York.

Goodyear, C. P. 1984. Analysis of the potential yield per recruit for striped bass produced in the Chesapeake Bay. North American Journal of Fisheries Management 4:488–496.

Hanski, I., and M. Gilpin. 1991. Metapopulation dynamics—brief history and conceptual domain. Biological Journal of the Linnean Society 42:3–16.

Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. Chapman and Hall, New York.

Holland, G. A. 1969. Age, growth, and mortality of races of English sole (*Parophrys vetulus*) in Puget Sound, Washington. Pacific Marine Fisheries Commission Bulletin 7:35–50.

Horness, B., and five coauthors. In press. Use of hockey stick regression for determination of sediment quality thresholds: aromatic hydrocarbons versus liver lesions in a benthic fish species (English sole, *Pleuronectes vetulus*). Environmental Toxicology and Chemistry.

Johnson, L. L., E. Casillas, T. K. Collier, B. B. McCain, and U. Varanasi. 1988. Contaminant effects on ovarian development in English sole (*Parophrys vetulus*) from Puget Sound, Washington. Canadian Journal of Fisheries and Aquatic Sciences 45:2133–2146.

Johnson, L. L., E. Casillas, T. K. Collier, J. E. Stein, and U. Varanasi. 1993a. Contaminant effects of reproductive success in selected benthic fish species. Marine Environmental Research 35:165–170.

Johnson, L. L., E. Casillas, M. S. Myers, L. D. Rhodes, and O. P. Olson. 1991. Patterns of oocyte development and related changes in plasma 17-B estradiol, vitellogenin, and plasma chemistry in English sole (*Parophrys vetulus* Girard). Journal of Experimental Marine Biology and Ecology 152:161–185.

Johnson, L. L., and J. T. Landahl. 1994. Chemical contaminants, liver disease, and mortality rates in English sole (*Pleuronectes vetulus*). Ecological Applications 4:59–68.

Johnson, L. L., M. S. Myers, D. Goyette, and R. F. Addison. 1994. Toxic chemicals and fish health in Puget Sound and the Georgia Strait. Canadian Technical Report of Fisheries and Aquatic Sciences 1948:304–329.

Johnson, L. L., G. Nelson, S. Sol, D. Lomax, and E. Casillas. 1997. Fecundity and egg weight in English sole (*Pleuronectes vetulus*) from Puget Sound, WA: influence of nutritional status and chemical contaminants. U.S. National Marine Fisheries Service Fishery Bulletin 95:231–249.

Johnson, L. L., and seven coauthors. 1993b. Chemical contaminants and hepatic lesions in winter flounder (*Pleuronectes americanus*) from the northeast coast of the United States. Environmental Science and Technology 27:2759–2771.

Ketchen, K. S. 1947. The age, growth, and mortality of the lemon sole (*Parophrys vetulus* Girard) on the British Columbia fishing grounds. Master's thesis. University of British Columbia, Vancouver.

Ketchen, K. S. 1956. Factors influencing the survival of the lemon sole (*Parophrys vetulus*) in Hecate Strait, British Columbia. Journal of the Fisheries Research Board of Canada, 13:647–694.

Ketchen, K. S., and C. R. Forrester. 1966. Population dynamics of the petrale sole (*Eopsetta jordani*) in waters off western Canada. Fisheries Research Board of Canada Bulletin 153.

Krahn, M. M., and five coauthors. 1986. Associations between metabolites of aromatic compounds in bile and the occurrence of hepatic lesions in English sole (*Parophrys vetulus*) from Puget Sound, Washington. Archives of Environmental Contamination and Toxicology 15:61–67.

Kroon, H. de, J. von Groenendael, A. Plaisier, and H. Caswell. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology 67:1427–1431.

Landahl, J. T., and L. L. Johnson. 1993. Contaminant exposure and population growth of English sole in Puget Sound: the need for better early life-history data. Pages 117–123 in L. A. Fuiman, editor. Water quality and the early life stages of fishes. American Fisheries Society, Symposium 14, Bethesda, Maryland.

Laroche, J. L., and S. L. Richardson. 1979. Winter–spring abundance of larval English sole, Parophrys vetulus, between the Columbia River and Cape Blanco, Oregon, during 1972–75, with notes on occurrences of three other pleuronectids. Estuarine Coastal and Marine Science 8:455–476.

Laroche, J. L., S. L. Richardson, and A. A. Rosenberg. 1982. Age and growth of a pleuronectid, Paropphrys vetulus, during the pelagic larval period in Oregon coastal waters. U.S. National Marine Fisheries Service Fishery Bulletin 80:93–104.

Lassuy, D. R. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest)—English sole. U.S. Army Corps of Engineers, Report 82(11.101)/TR EL-82-4, Slidell, Louisiana.

Lee, C.-K. C. 1972. The biology and population dynamics of the common dab (Limanda limanda L.) in the North Sea. Doctoral dissertation. University of East Anglia, Norwich, UK.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika 33:183–212.

Malins, D. C., and eleven coauthors. 1984. Chemical pollutants in sediments and diseases in bottom-dwelling fish in Puget Sound, Washington. Environmental Science and Technology 18:705–713.

Malins, D. C., and five coauthors. 1982. Chemical contaminants and abnormalities in fish and invertebrates from Puget Sound. NOAA (National Oceanic and Atmospheric Administration) Technical Memorandum OMPA (Office of Marine Pollution Assessment), OMPA-19, Boulder, Colorado.

Malins, D. C., B. B. McCain, D. W. Brown, A. K. Sparks, and H. O. Hodgins. 1980. Chemical contaminants and abnormalities in fish and invertebrates from Puget Sound. NOAA (National Oceanic and Atmospheric Administration) Technical Memorandum OMPA (Office of Marine Pollution Assessment), OMPA-2, Boulder, Colorado.

Malins, D. C., and seven coauthors. 1985. Toxic chemicals in sediments and biota from a creosote-polluted harbor: relationships with hepatic neoplasms and other hepatic lesions in English sole (Parophrys vetulus). Carcinogenesis 6:1463–1469.

Meador, J. P., and seven coauthors. 1994. National Status and Trends Program, National Benthic Surveillance Project: Pacific Coast. Analyses of elements in sediment and tissue, cycles I to V (1984–1988). NOAA (National Oceanic and Atmospheric Administration) Technical Memorandum NMFS (National Marine Fisheries Service) NWFSC-16. (Northwest Fisheries Science Center, Seattle.)

Menasveta, D. 1958. Migrations and fishing mortality of English sole (Parophrys vetulus) in Saratoga Passage and adjacent waters. Master's thesis. University of Washington, Seattle.

Myers, M. S., and five coauthors. In press. Toxicopathic hepatic lesions in subadult English sole (Pleuronectes vetulus) from Puget Sound, Washington, U.S.A.; relationships with other biomarkers of contaminant exposure. Marine Environmental Research.

Myers, M. S., J. T. Landahl, M. M. Krahn, L. L. Johnson, and B. B. McCain. 1990. Overview of studies on liver carcinogenesis in English sole from Puget Sound; evidence for a xenobiotic chemical etiology. I: pathology and epizootiology. Science of the Total Environment 94:33–50.

Myers, M. S., and six coauthors. 1994. Relationships between toxicopathic hepatic lesions and exposure to chemical contaminants in English sole (Pleuronectes vetulus), starry flounder (Platichthys stellatus) and white croaker (Genyonemus lineatus) from selected marine sites on the Pacific Coast, USA. Environmental Health Perspectives 102:200–215.

Myers, R. A., N. J. Barrowman, J. A. Hutchings, and A. A. Rosenberg. 1995. Population dynamics of exploited fish stocks at low population levels. Science 269:1106–1108.

Myers, R. A., and N. G. Cadigan. 1993. Density-dependent juvenile mortality in marine demersal fish. Canadian Journal of Fisheries and Aquatic Sciences 50:1576–1590.

Orsi, J. 1968. The embryology of the English sole, Parophrys vetulus. California Fish and Game 54:133–135.

Pitt, T. 1973. Assessment of American plaice stocks on the Grand Bank, ICNAF Divisions 3C and 3N. International Commission for the Northwest Atlantic Fisheries Research Bulletin 10:64–77.

PSWQA (Puget Sound Water Quality Authority). 1987. Puget Sound environmental atlas. Puget Sound Estuary Program, Olympia, Washington.

PSWQA (Puget Sound Water Quality Authority). 1992a. Puget Sound update: third annual report of the Puget Sound Ambient Monitoring Program. PSWQA, Olympia, Washington.

PSWQA (Puget Sound Water Quality Authority). 1992b. Puget Sound environmental atlas update. Puget Sound Estuary Program, Olympia, Washington.

PSWQA (Puget Sound Water Quality Authority). 1993. Puget Sound update: fourth annual report of the Puget Sound Ambient Monitoring Program. PSWQA, Olympia, Washington.

Schaaf, W. E., D. S. Peters, D. S. Vaughan, L. Coston-Clements, and C. W. Krouse. 1987. Fish population responses to chronic and acute pollution: the influence of life history strategies. Estuaries 10:267–275.

Schmitt, C., S. Quinnell, M. Rickey, and M. Stanley. 1991. Groundfish statistics from commercial fish-

eries in Puget Sound. Washington, Department of Fisheries, Progress Report 285, Olympia.

Schmitt, C., J. Schweigert, and T. P. Quinn. 1994. Anthropogenic influences on fish populations of the Georgia Basin. Canadian Technical Report of Fisheries and Aquatic Sciences 1948:218–229.

Sissenwine, M. P., and J. G. Sheperd. 1987. An alternative perspective on recruitment overfishing and biological reference points. Canadian Journal of Fisheries and Aquatic Sciences 44:913–918.

Stein, J. E., and five coauthors. 1992. Bioindicators of contaminant exposure and effects: studies with benthic fish in Puget Sound, Washington. Environmental Toxicology and Chemistry 11:701–714.

Toole, C. L., R. A. Barnhart, and C. P. Onur. 1987. Habitat suitability index models: juvenile English sole. U.S. Fish and Wildlife Service Biological Report 82(10.133).

Usher, M. B. 1972. Developments in the Leslie matrix model. Pages 29–60 in J. N. R. Jeffers, editor. Mathematical models in ecology. Blackwell Scientific Publications, Oxford, UK.

Van Cleve, R., and S. Z. El-Sayed. 1969. Age, growth, and productivity of an English sole (*Parophrys vetulus*) population in Puget Sound, Washington. Pacific Marine Fisheries Commission Bulletin 7:51–71.

Varanasi, U., and ten coauthors. 1989. National Benthic Surveillance Project: Pacific Coast. Part II: technical presentation of the results for cycles I to III (1984–86). NOAA (National Oceanic and Atmospheric Administration Technical Memorandum) NMFS (National Marine Fisheries Service) F/NWC-170. (Northwest Fisheries Science Center, Seattle.)