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Preliminary Mass-Balance Model of Prince William Sound, Alaska, for the Pre-Spill Period, 1980-1989

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ABSTRACT

A mass-balance model of trophic interactions among the key functional groups of Prince William Sound (PWS), Alaska, is presented, based mainly on published data referring to the period from 1980 to 1989, before the *Exxon Valdez* oil spill.

The functional groups explicitly included in the model are: detritus, phytoplankton, macroalgae, small zooplankton, large zooplankton, epifaunal benthos, infaunal benthos, intertidal invertebrates, demersal fish, herring, salmon fry from hatcheries, wild salmon fry, salmon, other pelagic fishes, birds, sea otters, other resident marine mammals, and transient marine mammals.

Balancing of the model required few steps that went beyond the available data; nevertheless, the model is preliminary in that additional ecological information is available on PWS and the functional groups of the organisms therein. Much of this information is not yet incorporated in the model. However, the purpose of this model is to serve as basis for further work, illustrated in two authored appendices, one showing the close match between the trophic levels estimated by the models and estimates based on stable isotope ratios, and the other documenting how inferences on the dynamics of PWS may be derived from its static representation.

Director's Foreword

The first Mass-balance models of marine ecosystems in the North-eastern Pacific, covering the Alaska Gyre, the shelf of southern British Columbia, and the Strait of Georgia, were constructed in November of 1996 at a workshop held at the UBC Fisheries Centre (*see* Fisheries Centre Research Report 1996, Vol. 4, No 1). The present report extends that work by drawing up a preliminary ecosystem model of Prince William Sound, Alaska, in its most likely form prior to the Exxon Valdez oil spill in 1989. ECOPATH models are forgiving in that they can be improved and enhanced using new information without having to be completely reinvented. This report puts forward a preliminary model, based on data from published literature, whose sole purpose is to lead to an improved model based on more complete and more accurate data from the recent intensive work in Prince William Sound.

For many years single species stock assessment of fisheries has reigned supreme and separate from mainstream marine ecology, but, for marine conservation, this approach and lack of integration has been conspicuously unable to answer the crucial questions of our time. These questions include the interplay of predators, competitors and prey with human fisheries, the impact both acute and chronic of marine pollution, and the effects of progressive shoreline development on the stability and value to human society of coastal ecosystems.

ECOPATH is a straightforward trophic modeling approach to ecosystems, that balances the budget of biomass production and loss for each component in the system by solving a set of simultaneous linear equations. The ECOPATH approach is the only ecosystem model to obey the laws of thermodynamics. It is based on pioneering work by Dr Geoffrey Polovina from Hawaii in the early 1980s, and developed by Dr Daniel Pauly when he was at ICLARM, Manila, and Dr Villy Christensen from Denmark. Dr Carl Walters at the Fisheries Centre recently developed ECOSIM a dynamic version of ECOPATH.

A Preliminary Mass-Balance Model of Prince William Sound, Alaska, for the Pre-Oilspill Period, 1980-1989 is the latest in a series of research reports published by the UBC Fisheries Centre. The series aims to focus on broad multidisciplinary problems in fisheries management, to provide an synoptic overview of the foundations and themes of current research, to report on work-in-progress, and to identify the next steps and ways that research may be improved. Edited reports of the workshops and research in progress are published in *Fisheries Centre Research Reports* and are distributed to all project or workshop participants. Further copies are available on request for a modest cost-recovery charge. Please contact the Fisheries Centre mail, fax or email to 'office@fisheries.com'.

Tony J. Pitcher
Professor of Fisheries
Director, UBC Fisheries Centre

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INTRODUCTION

Prince William Sound

Prince William Sound (PWS), located near the northern apex of the Gulf of Alaska and renown for its wildlife and once pristine environment, became the center of the world's attention on March 24, 1989, when the supertanker Exxon Valdez ran aground on Bligh Reef, in the Northeastern part of the Sound (Fig.1), spilling over 40 million liters of crude oil - the largest oil spill in United States history. During the first two weeks following the spill, the oil was transported the southwest through the western part of PWS, and into the Gulf of Alaska, along the Kenai Peninsula, killing thousands of seabirds, marine mammals and vast numbers of fish and invertebrates (Loughlin 1994).

Early assessments of the impact of the *Exxon Valdez* oil spill (EVOS) were presented in the proceedings, edited by Rice et al. (1996), of a symposium held from February 2 to 5, 1993. Major efforts have been made since, under the guidance of the Exxon Valdez Oil Spill Trustee Council, to study the long-term effects of the EVOS, and a second generation of assessments is now emerging which will address questions left open at the 1993 symposium.

The present report is designed to support these efforts by presenting a preliminary version of what will be more precise and realistic models of trophic interactions among the major functional groups of PWS, for the periods before and after the spill. These models will incorporate as much of the relevant data from both periods as possible, for a large number of functional groups.

However, the model presented herein, and the assumptions used for its construction are preliminary. We are aware of the existence of better data for most of the functional groups in the model. A primary goal of the current effort is a collaborative partnership among PWS experts to incorporate these better data thereby maximizing the usefulness of the more detailed models, to be constructed in 1998.

Pending these detailed models, the preliminary model presented here was assembled to :

1) document the approach used in constructing mass-balance models, and the type of data required;
2) introduce the Ecopath software for construction of such models; and
3) determine whether sufficient data are available for constructing a balanced model for the less investigated pre-spill period, and an improved model, covering the post-spill period.

PWS consists of a central basin, with a maximum depth of 800 m, surrounded by islands, fjords, bays, and a large tidal estuary system (Fig. 1); the mean water depth is 300 m (Cooney 1993, Loughlin 1994). The semi-enclosed nature of PWS justifies the application of a modeling approach, such as Ecopath (Box 1), that assumes mass-balance among the various elements of the system, and limited (or at least well-quantified) exchanges with adjacent systems (see also contributions in Pauly and Christensen 1996).

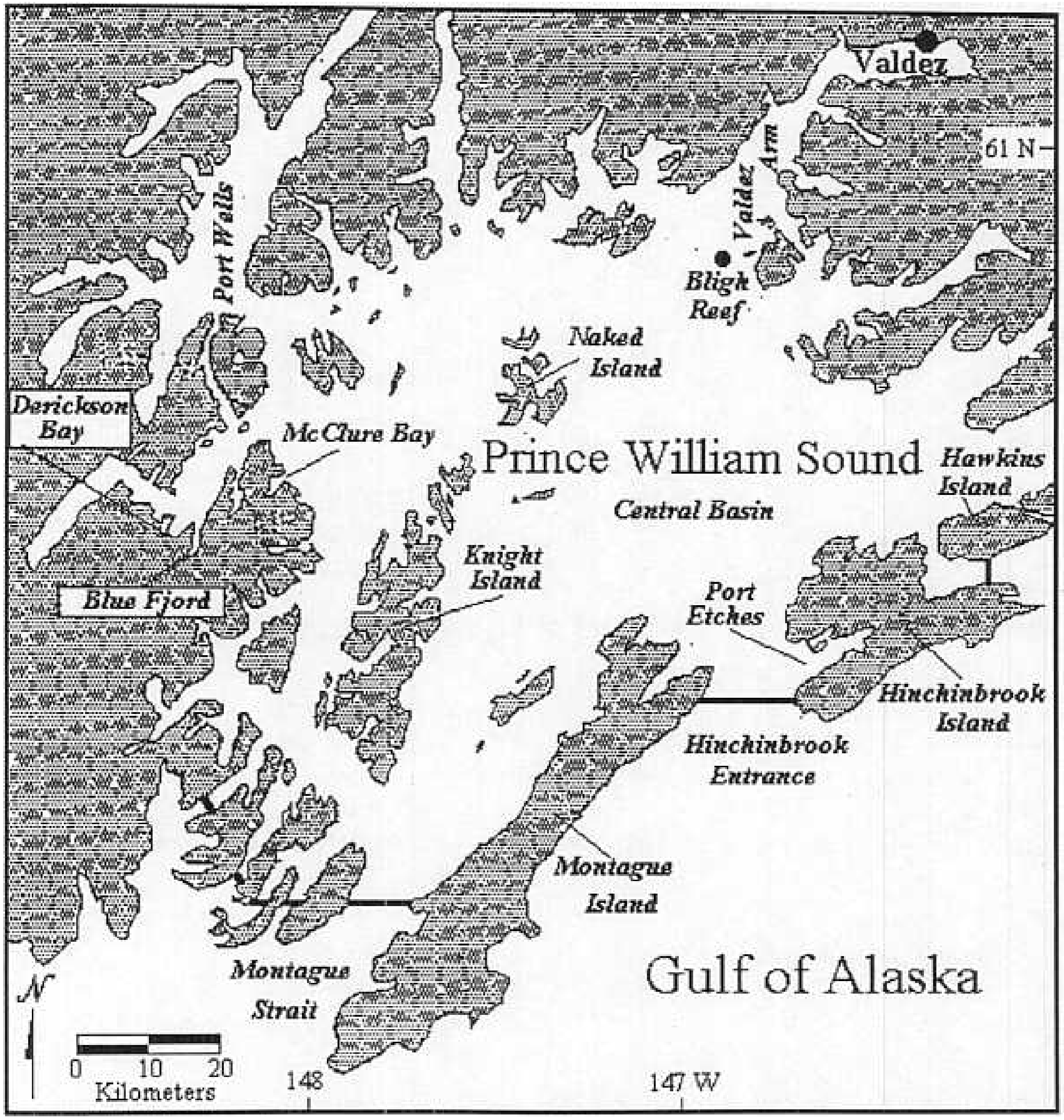

Figure 1. Map of Prince William Sound, Alaska, showing locations mentioned in the text (modified from Sturdevant et al.1996).

The Ecopath approach and software

The Ecopath approach and software were initially developed by Polovina (1984, 1995), of the U.S. National Marine Fisheries Service (Honolulu Laboratory). V. Christensen and D. Pauly, then both at the International Center for Living Aquatic Resources Management (ICLARM), improved on this work (see Christensen and Pauly 1992a), and made it widely available in the form of a well-documented software for computer running MS-DOS (Christensen and Pauly 1992b), and later Windows (Christensen and Pauly 1995, 1996). Both versions allow rapid construction and verification of mass-balance models of ecosystems. The steps involved consist essentially of:

(i) Identification of the area and period for which a model is to be constructed;

(ii) Definition of the functional groups (i.e., 'boxes') to be included;

(iii) Entry of a diet matrix, expressing the fraction that each 'box' in the model represents in the diet of its consumers;

(iv) Entry of food consumption rate, of production/biomass ratio or of biomass, and of fisheries catches, if any, for each box;

(v) Balance the model, or modify entries (iii & iv) until input = output for each box;

(vi) Compare model outputs (network characteristics, estimated trophic levels and other features of each box) with estimates for the same area during another period, or with outputs of the same model type from other, similar areas, etc.

Box 1. Basic equations, assumptions and parameters of the Ecopath approach

The mass-balance modeling approach used in this workshop combines an approach by Polovina and Ow (1983) and Polovina (1984, 1985) for estimation of biomass and food consumption of the various elements (species or groups of species) of an aquatic ecosystem (the original 'ECOPATH') with an approach proposed by Ulanowicz (1986) for analysis of flows between the elements of ecosystems The result of this synthesis was initially implemented as a DOS software called 'ECOPATH II', documented in Christensen and Pauly (1992a, 1992b), and more recently in form of a Windows software, Ecopath 3.0 (Christensen and Pauly 1995, 1996). Unless noted otherwise the word 'Ecopath' refers to the latter, Windows version. The ecosystem is modeled using a set of simultaneous linear equations (one for each group i in the system), i.e.

Production by (i) - all predation on (i) - nonpredation losses of (i) - export of (i) = 0, for all (i).

This can also be put as

$$P_i\text{-}M2_i - P_i(1\text{-}EE_i) - EX_i = 0 \qquad \ldots 1)$$

where P_i is the production of (i), $M2_i$ is the total predation mortality of (i), EE_i is the ecotrophic efficiency of (i) or the proportion of the production that is either exported or predated upon, $(1\text{-}EE_i)$ is the "other mortality", and EX_i is the export of (i).

Equation (1) can be re-expressed as

$$B_i{*}P/B_i - \Sigma_j B_j{*}Q/B_j{*}DC_{ij}\text{-}P/B_i{*}B_i(1\text{-}EE_i)\text{-}EX_i=0 \qquad \ldots 1)$$

or

$$B_i{*}P/B_i{*}EE_i - \Sigma_j B_j{*}Q/B_j{*}DC_{ij} - EX_i = 0 \qquad \ldots 2)$$

where B_i is the biomass of (i), P/B_i is the production/biomass ratio, Q/B_i is the consumption/biomass ratio and DC_{ij} is the fraction of prey (i) in the average diet of predator (j).

Based on (2), for a system with n groups, n linear equations can be given in explicit terms:

$$B_1P/B_1EE_1 - B_1Q/B_1DC_{11}\text{-}B_2Q/B_2DC_{21} - \ldots\text{-}B_nQ/B_nDC_{n1} - EX_1 = 0$$

$$B_2P/B_2EE_2 - B_1Q/B_1DC_{12} - B_2Q/B_2DC_{22} - \ldots\text{-}B_nQ/B_nDC_{n2} - EX_2 = 0$$

$$B_nP/B_nEE_n - B_1Q/B_1DC_{1n} - B_2Q/B_2DC_{2n} - \ldots\text{-}B_nQ/B_nDC_{nn} - EX_n = 0$$

This system of simultaneous linear equations can be solved through matrix inversion. In Ecopath, this is done using the generalized inverse method described by MacKay (1981), which has features making it generally more versatile than standard inverse methods.

Thus, if the set of equations is overdetermined (more equations than unknowns) and the equations are not consistent with each other, the generalized inverse method provides least squares estimates which minimize the discrepancies. If, on the other hand, the system is undetermined (more unknowns than equations), an answer that is consistent with the data (although not unique) will still be output.

Generally only one of the parameters B_i, P/B_i, Q/B_i, or EE_i may be unknown for any group i. In special cases, however, Q/B_i may be unknown in addition to one of the other parameters (Christensen and Pauly 1992b). Exports (e.g., fisheries catches) and diet compositions are always required for all groups.

A box (or "state variable") in an Ecopath model may be a group of (ecologically) related species, i.e., a functional group, a single species, or a single size/age group of a given species.

These steps can be implemented easily if basic parameters can be estimated (see also Box 1), especially as numerous well-documented examples exist of Ecopath applications to aquatic ecosystems (see Pauly and Christensen 1993, and contributions in Christensen and Pauly 1993). We refer here frequently to three ecosystems that have much in common with PWS (the Strait of Georgia, the coast of British Columbia, and the Alaska gyre), documented through the contributions in Pauly and Christensen (1996), and from which many parameter estimates were taken. In the following pages, details are provided, by functional group, on how items (ii) to (vi) were implemented, following definition of the period (1980-1989) and area to be modeled (Fig 1).

This is then followed by two authored appendices, by Kline and Pauly (1997; Appendix 1) and Pauly and Dalsgaard (1997; Appendix 2), illustrating some of the possible follow ups to the preliminary model documented here.

PRELIMINARY MODEL INPUTS

Phytoplankton

The phytoplankton community in PWS is usually dominated by diatoms. However, Goering et al. (1973) found that in Valdez Arm (Fig. 1), the flagellate *Phaeocystis pouchetii* was numerically dominant during April; also, during the less productive July conditions, the phytoplankton community was dominated by the dinoflagellate *Ceratium longipes*.

Detailed seasonal data on phytoplankton growth exist for selected areas of PWS. Chl. *a* concentrations and carbon production were measured bimonthly from May 1971 to April 1972 in Port Valdez and Valdez Arm. A typical spring-bloom sequence was found in which both standing crop and primary production increased rapidly in April, depleting nitrate from the upper water layers. Production then de creased during the reminder of the Summer, then increased again - at least in several areas - in the Fall (Sambrotto and Lorenzen 1986).

The mean yearly primary production of ~185 $gC \cdot m^{-2}$ estimated by Sambrotto and Lorenzen (1986), may be assumed to apply to the whole of PWS (Cooney 1986), as the range is 150-200 $g\ C \cdot m^{-2} \cdot year^{-1}$ (T. Cooney, pers. comm.). Assuming 0.1 gC ≈ 1g ww, an annual primary production of 185 $gC \cdot m^{-2}$ equals 1850 t $ww \cdot km^{-2} \cdot year^{-1}$.

Olivieri et al. (1993) estimated the P/B ratios of large diatoms and small phytoplankton (cells < 5 μm; including cyanobacteria and flagellates) to range from 125 to 255 $year^{-1}$, with a mean of 190 $year^{-1}$. From this, the phytoplankton biomass can be estimated as (1850 t $ww \cdot km^{-2} \cdot year^{-1}$) / (190 $year^{-1}$) ≈ 10 t $ww \cdot km^{2}$.

Macroalgae

In PWS, dense macrolagal assemblages are typical in the shallow subtidal zone, which extends from the intertidal zone to depths of about 20m (Dean et al. 1996).

Dean et al. (1996) compared the density and biomass of subtidal macroalgae in oiled versus non-oiled (control) sites in PWS one year after the Exxon Valdez oil spill. While the relative species composition of these assemblages appeared to have changed, the authors' study revealed no differences in total density, biomass, or percent cover. These results provide some justification for using the biomass values of this study's control locations for a pre-spill baseline reference Use of these values assumes that they are representative of the shallow subtidal zone of the entire PWS for the entire decade from 1980 to 1989, prior to the oil spill.

Table 1. Macroalgae biomass estimates for different PWS habitats[a].

Habitats	Biomass ($g\ ww \cdot m^{-2}$) Shallow	Deeper
Bays	1,766	529
Points	2,690	678
Nereocystis	6,240	-
Means	3,565	402

a) Modified from Dean et al. (1996).

Three type of habitats were identified by Dean et al. (1996):

1. *Agarum-Laminaria* beds in bays(2-11m, 11-20m);
2. *Agarum-Laminaria* beds on points (2-11m, 11-20m); and
3. *Nereocystis* beds (2-8m).

It is assumed here that each of these habitats cover 1/3 of the shallow subtidal zone (0 - 20 m) of PWS. Furthermore, we assume that the shallow subtidal zone is 1/10 of the surface area of PWS. Since PWS has a surface area of approximately 8800 km^2, the shallow subtidal zone is 880 km^2 . These assumptions are being revised during the next iteration to account for areas with no kelp cover and by decreasing the areal proportion of shallow subtidal zone in PWS using GIS measurements.

Dean et al. (1996) found *Agarum cribrosum* and *Laminaria saccharina* to be the dominant subtidal macroalgae in sheltered bays. Generally, these two species constituted more than 90% of total macroalgal biomass.

Agarum cribrosum also dominated on exposed points (more than 60 % in terms of number of individuals). Less abundant algae were *Laminaria saccharina* and *L. groenlandica.*

Nereocystes habitats are located on exposed sites, and the algal diversity was higher than in the other two habitats. The kelp forest structure at these locations consists of a canopy of *Nereocystes luetkeana* with an understory *of L. groenlandica* (61 % of the biomass), *L. yezoensis, Pleurophycus gardneri, and A. cribrosum.*

Based on the aforementioned assumptions, the biomass of macroalgae was calculated to be 3,967 $g \cdot m^{-2}$ for 880 km^2 of shallow subtidal area; re-expressed for the PWS as a whole, this corresponds to ~ 400 $t \cdot km^{-2}$.

Estimates of the P/B ratio of PWS macroalgae were not found. The value of 4.4 $year^{-1}$ used here, pertaining to *Laminaria* beds in the North Atlantic, is from Brady-Campbell et al. (1984).

Detritus

Rough estimates of the standing stock of detritus in marine ecosystems may be obtained from:

$$\boxed{\log_{10} D = -2.41 + 0.954 \cdot \log_{10} PP + 0.863 \log_{10} E}$$

where D is the standing stock of detritus, in $gC \cdot m^{-2}$, PP the primary production in $gC \cdot m^{-2} \cdot year^{-1}$, and E is the euphotic depth in meters (Pauly et al. 1993). In the absence of a readily available estimates of mean euphotic depth for PWS, the detritus standing stock estimated by this equation for the Strait of Georgia, of 7 $t \cdot km^{-2}$ (Venier 1996), is used. The precise value of this estimate has no effect on the computation of detritus flows.

Bacteria (incl. bacterioplankton) are not included in the model: it is assumed that bacteria consume only detritus, and that the fluxes associated with this consumption can be treated as if they occurred in another, adjacent ecosystem, i.e., that in which detritus accumulates when it leaves PWS. This omission of bacterial fluxes has no impact whatsoever on the other estimates of fluxes estimated by Ecopath.

Zooplankton

In March-May, the upper layer of zooplankton in PWS is dominated by the copepods *Neocalanus cristatus, N. plumchrus, Eucalanus bungii,* which are oceanic species, by *Calanus marshallae, Pseudocalanus* spp which are not, and by the arrow-worm *Sagitta elegans*. Towards June, this community is gradually replaced by late stage copepodites of *Calanus marshallae*, the smaller copepods *Acartia, Centropages, Tortanus* and *Pseudocalanus, Metridia okhotensis, M. pacifica*, and the cladocerans *Podon* and *Evadne*. In the Fall and Winter, these are followed by *Sagitta elegans* and *M. pacifica*. Other groups also occurring in zooplankton samples are amphipods, euphausiids (5 species), and coelenterates, among others (Anon 1980; Cooney 1986; Cooney 1993; Ted Cooney, pers. comm.).

Table 2. Mean settled zooplankton volume, upper 20m of PWS (T. Cooney, pers. comm.)[a]

Year	$ml \cdot m^{-3}$
1981	1.45
1982	2.43
1983	2.65
1984	2.39
1985	4.48
1986	1.53
1987	1.42
1988	0.91
1989	5.2
Mean	1.75

a) Sampled using a 0.25 mm mesh size and 0.5 m diameter net. The data are average values for March 15 to June 15, and were taken 2-3 times weekly in the southern part of the Sound.

Published estimates of zooplankton biomass could not be found for the period prior to the EVOS, and we therefore relied on the data in Table 2, made available by Dr T. Cooney (pers. comm.):

Settled volumes in $ml \cdot m^{-3}$ can be converted to $g \cdot m^{-3}$ by assuming that 70% of settled volume in milliliters is equivalent to wet weight in grams (Weibe et al. 1975). Applying this conversion factor, 1.75 $ml \cdot m^{-3}$ correspond to 1.225 $g\ ww \cdot m^{-3}$.

Given that PWS on average is 300m deep, and that zooplankton occur at the same density throughout the water column, the biomass of zooplankton per surface area would be: 1.225 $g \cdot m^{-3} \cdot 300m = 368\ g \cdot m^{-2}$.

For the model, it is assumed that 25% of zooplankton biomass consists of macroplankton, based on Cooney (1993), who gave 25% as a conservative estimate of macroplankton production to total zooplankton production. The remaining 75 % are assumed to consists overwhelmingly of mesoplankon (microzooplanton is not considered here). This leads to biomass estimates of 92 $t \cdot km^{-2}$ for macroplankton and 276 $t \cdot km^{-2}$ for mesoplankton.

Another input required by Ecopath is Q/B, here assumed to have the same value, 10.5 $year^{-1}$, as herbivorous zooplankton in the Strait of Georgia (Harrison et al. 1983). Finally, we assume mesozooplankton to have a diet consisting only of phytoplankton, while macrozooplankton is assumed to consume 75% mesozooplankton and 25% phytoplankton. For both zooplankton groups, we set EE at 0.95, a default value for groups heavily preyed upon (Polovina 1984).

Benthic invertebrates

The values used herein for benthic invertebrates larger than 0.5 mm are very tentative. Estimates for these components need considerable refinement.

To account for substrate and other habitat differences, PWS was split into the following three areas with generally different habitat characteristics. For this initial exercise, one third of the surface area was allocated to each area.

1. Central Basin and Hinchinbrook Entrance;
2. Eastern fjords and bays;
3. Western fjords and bays.

The substratum in the central basin (1) is composed of sand, silt and clay, reflecting a depositional environment. The fjords in the west of PWS (3) are impacted by glacial silt, and characterized by low infaunal abundance and biomass, at least when compared to the communities in the east and north of PWS. Here, muddy bottoms dominate, supporting a primarily deposit-feeding infauna (Feder and Jewett 1986). Table 3 and 4 shows the estimated biomass of benthic infauna and benthic epifauna respectively.

Table 3a. Estimated biomass of benthic infauna, in PWS (from Feder and Jewett 1986).

Area	Biomass ($t \cdot km^{-2}$)	Functional groups (% weight)
Central Basin	417	Deposit feeders (66.8), Suspension feeders (26.8), Scavengers & predators (6.4)
Eastern fjords & bays	246[a]	Polychaetes, mollusks, echinoderms, crustaceans
Western fjords & bays	10.5[b]	Polychaetes (dep. feed.), Bivalves (dep. feed.), Suspension feeders
Mean	225	---

a) Port Valdez and Valdez Arm;
Derickson Bay (20 $g \cdot m^{-2}$); Blue Fjord (13 & 3 $g \cdot m^{-2}$); and McClure Bay (6 $g \cdot m^{-2}$).

Feder and Jewett (1986, Table 12-9) indicate that the infaunal biomass at Hinchinbrook Entrance, of 343 $g \cdot m^{-2}$, produces 4.6 $gC \cdot m^{-2} \cdot year^{-1}$, corresponding to 222 g $ww \cdot m^{-2} \cdot year^{-1}$.

Table 3b. Estimated biomass of benthic epifauna, PWS (from Feder and Jewett 1986).

Area	Biomass ($t \cdot km^{-2}$)	Species (group) (% weight)
Central basin	2.4	Tanner crab (67), Pink shrimp (7), Mud star (5), Other groups (21)
Eastern fjords & bays[a]	0.8	Sunflower star (62), Pink shrimp (28), Tanner crab (4), Mollusks (0.2), Others groups (5.8)
Western fjords & bays	0.8[b]	n.a.
Mean	1.3	---

a) Near Port Etches;
b) No estimate available; biomass assumed to be the same as for eastern fjords and bays.

This leads to a P/B estimate of 0.6 $year^{-1}$, which we apply throughout PWS. The same table in Feder and Jewett (1986) gives a P/B ratio of 2.0 $year^{-1}$ for the epifaunal macrofauna, here also applied to the entire PWS.

Trowbridge (1996) gives the following catchesof benthic invertebrates from PWS:

1) Epifauna (including pink and other shrimps), king crab (red, blue, brown), and tanner crab: 0.143 $t \cdot km^{-2} \cdot year^{-1}$;
2) Infauna (razor clam and others): 0.003 $t \cdot km^{-2} \cdot year^{-1}$.

It is here assumed that similar catches were made in the 1980-1989 period.

Intertidal invertebrates

Intertidal invertebrates, dominated by barnacles, gastropods, and bivalves (especially *Mytilus edulis*), are, in PWS, an important source of food for birds and sea otters, among others predators. The only biomass estimate we have identified, 624 $g \cdot m^{-2}$, is from Stekoll et al. (1996, Table 2), and was obtained during a study carried out from the Spring of 1990 to the Summer 1991, to assess the impact on the intertidal zone of the EVOS, and of the cleanup efforts which followed.

Assuming the intertidal zone makes up 1% of the surface area of PWS, the total size of the zone is 88 km^2. Averaged over the total area of PWS, the invertebrate biomass is 6.24 $t \cdot km^{-2}$. P/B and Q/B are assumed equal to the values for epifaunal benthos (see above).

Table 4. Q/B estimates[a] and diet matrix [b] (% weight) of PWS zoobenthos.

Zoobenthos	Q/B ($year^{-1}$)	Inf.	Epif.	Detrit.	Zoopl.	M. algae
Infauna	23	10	10	60	20	-
Epifauna	10	30	20	30	10	10

a) From Guénette (1996, based on several sources);
Based on Table 3a for infauna (mainly deposit feeders) and Table 3b for epifauna (mainly predators: tanner crab is a scavenger/predator; pink shrimp feed on small polychaetes and crustaceans; and sunflower feed mainly on mollusks).

O'Clair and Zimmerman (1986, Table 11-4) list the following feeding groups of intertidal benthos of rocky areas of the Gulf of Alaska: herbivores (22%), suspension feeders (23%), carnivores (26%), deposit feeders (16%), omnivores (6%), and scavengers (7%).

Demersal fish

Demersal fish, as defined here, includes true bottom fish such as flatfish and skates and semi-demersal fish such as pacific cod, walleye pollock and others.

In PWS, the two dominant demersal fish species are arrowtooth flounder and walleye pollock. Table 5 shows the biomass estimates resulting from a trawl survey conducted in PWS in 1989. As reported by NMFS (1993), "arrowtooth flounder made up the greatest proportion of total biomass at every site except Central Basin and Port Wells. It accounted for 67% of total biomass in the area of Knight Island/Montague Strait and 65% of total biomass in the area outside PWS" (NMFS 1993). Based on this, arrowtooth flounder was set to contribute 60% of total demersal biomass in Table 5.

Based on Table 5, the density of demersal fish in PWS was calculated as: 83,000 tonnes / 8800 km^2 = 9.4 $t \cdot km^{-2}$

Pending detailed analyses of data from PWS, the P/B value of 1 $year^{-1}$, and the Q/B value of 4.24 $year^{-1}$, pertaining to the demersal fishes of the Strait of Georgia, were taken from Venier (1996, Table 36).

No suitable data set being available for the period prior to 1987, the catches used here are simple averages for 1987 and 1988 (Table 6). These suggest, for PWS as a whole, a catch of demersal fishes of 0.037 $t \cdot km^{-2} \cdot year^{-1}$.

Table 5. Estimated biomass of demersal fish species in PWS, 1989[a].

Species	Biomass (tonnes)	95% confidence interval
Arrowtooth flounder	50,000	6,000-90,000
Walleye pollock	9,500[c]	6,000-13,000
Flathead sole	8,000[c]	-
Sablefish	4,000[c]	1,000-8,000
Other species[b]	11,500[d]	-
Total	83,000	-

a) Adapted from NMFS (1993);
b) Big skate, Bering skate, Alaska skate, Aleutian skate, Pacific halibut, rex sole, Pacific cod, rougheye rockfish and others;
c) Based on the 95% confidence interval (walleye pollock and sablefish) and the fact that the walleye pollock biomass was only slightly greater than that of flathead sole (NMFS 1993);Based on arrowtooth flounder contributing 60% of total biomass

Table 6. Mean demersal fish catch from PWS, 1987-1988

Species	Catcht ($t \cdot year^{-1}$)
Rockfish	45.631
Sablefish	93.576
Pacific cod	174.780
Flatfish	9.663
Lingcod	0.439
Other	4.948
Total	329.037

Adapted from Bechtol (1995).

Adult halibut and cod are apex predators, and feed on a variety of medium to large fish such as pollock, flatfish, and sculpins. They also feed on invertebrates, such as crabs, shrimps and krill, and small pelagic fishes such as smelt. Walleye pollock and many rockfish species feed predominantly on small to medium-size nektonic prey such as large amphipods, copepods, krill, smelt, and other small fish. Pollock is also known to be cannibalistic. Sablefish is an omnivore and scavenger feeding on fish and invertebrates. Flatfish and sculpins have overwhelmingly benthic diets. Soles consume small invertebrates (worms, snails, clams, brittlestars, etc.), while flathead sole feed on shrimp, krill, herring, and smelt (Alton 1981).

Based on such feeding habits information, as well as diet information presented in various contributions in Pauly and Christesen (1996), the following diet composition was derived for the demersal fish of PWS (in % weight): benthic invertebrates (25); pelagic fish (25); macrozooplankton (15); mesozooplankton (15); herring (10); and demersal fish (10; cannibalism).

Herring

Herring spawns in PWS in Spring, from mid-April to early May (Morstad et al. 1996). This is also the season for seine and gill net fisheries, for sac roe, and for two spawn-on-kelp fisheries. Another fishery, for food and bait, occurs in the Fall. Table 7 presents mean catches for the period from 1980 to 1988.

Based on Table 7, the catch of herring in PWS equals 1.136 $t \cdot km^{-2}$;

The corresponding biomass, also for the 1980-1988 period, was estimated as 71,341 t or 8.107 $t \cdot km^{-2}$, based on an age-structured analysis (Morstad et al. 1996, Appendix H.11).

Given that, under equilibrium, F = catch/biomass, a fishing mortality (F) of 0.14 $year^{-1}$ can be estimated from the above figures. Natural mortality (M) was estimated as 0.53 $year^{-1}$, as the means of age-specific estimates (age 3 to 8) for herring in the Gulf of Alaska (Wespestad and Fried 1983). Since P/B, under equilibrium, equals total mortality (Z; Allen 1971), and Z = F + M, the P/B ratio for herring can be estimated from 0.53 + 0.14 = 0.67 $year^{-1}$.

The value of Q/B used here, of 18 $year^{-1}$, is the same as that used for small pelagics (mainly herring) in the Strait of Georgia (Venier 1996); the diet consists of zooplankton: euphausiids, copepods, mysids, and amphipods, among other (Whitehead 1985) .

Table 7. Average harvest of herring in PWS from 1980 to 1988.[a]

Fishery	Mean catch ($t \cdot year^{-1}$)
Seine and gillnet	7586
Spawn-on-kelp, natural	819
Spawn-on-kelp, pounds	538
Food and bait	1053
Total	9996

From Morstad et al. (1996).

Salmon fry

Both wild fry and hatchery-released salmon fry occur in PWS. The hatchery released fry is mostly pink salmon, which are believed to reside in the Sound from early April to July/early August (the hatchery stock is released in late April/early May). Table 8 summarizes key feature of salmon fry in PWS.

Initially, salmon fry consume mesoplankton; calanoid copepods are a preferred prey, but diversity of the diet increases with size of the fish (Cooney et al. 1978). For the present model, it will be assumed that the diet of young salmon consists of 75% mesoplankton and 25% macroplankton; also EE was set as 0.78 for wild fry and 0.63 for hatchery released fry (see section on 'Balancing the model').

Table 8. Characteristics of wild salmon fry, and hatchery released fry[a]

Parameters	Wild fry	Hatchery fry
Abundance (million)	500	300[c]
Density ($t \cdot km^2$)[b]	0.014	0.009
Survivors after 120 days (%)	22	37
Consumption (t) in 120 days	4979	4,513
Q/B ($year^{-1}$)	40	60

a) From Cooney (1993); both wild and hatchery released fry are about 25 g, and remain in PWS for 120 days when entering PWS;
b) Assuming that fry are evenly distributed within PWS; Mean release of (mainly) pink salmon, 1980-1989 (Morstad et al. 1996).

Adult Salmon

Adult salmon appear in PWS from June through September, while on their spawning runs. All parameters in the text below were therefore subsequently corrected to a yearly average as required for the model (multiplied by 4/12).

Table 9 shows the average harvest of salmon in the Sound from 1980 to 1989.

From Table 9, the average catch of salmon per area of PWS for the period 1980-1989 is calculated as 4.2 $t \cdot km^{-2}$.

Table 10 presents minimum estimates of the mean biomass of hatchery and wild pink and chum salmon in PWS from 1980 to 1989, based on wild stock escapement (minimum estimates), hatchery returns and catches.

Biomass estimates for the three other salmon species in PWS could not be found. However, pink salmon is the dominant species, contributing about 83% of the catch (in weight), while chum contributes about 13%. Assuming the same percentages apply to the biomas, the mean total standing stock of salmon in PWS (wild and hatchery) from 1980 to 1989 was 42,000 tonnes, or about 5 $t \cdot km^{-2}$.

Total mortality estimates for the oceanic phase of the various species of salmon caught in PWS are given in Table 11; their weighted mean is 2.37 $year^{-1}$, which serves as our estimate of P/B for salmon as a

Table 9. Catches of salmon in PWS, based on data from 1980 to 1989 (commercial and subsistence fishery).

Species	Catch (kg)	Catch[a] (number)	Mean wt (kg)[b]
Chinook	8,457	755	11.2
Sockeye	974,014	374,621	2.6
Coho	173,794	41,380	4.2
Pink	30,487,004	19,054,377	1.6
Chum	4,908,645	1,363,512	3.6
Total	36,551,913	20,834,645	(1.8)

a) Average catches in PWS from 1980 to 1989, based on Morstad et al.
(1996, Appendices E.2 & G.2);
Weighted means, based on Morstad et al. (1996, Appendix A.5).

Table 10. Estimated standing stock of hatchery and wild pink and chum salmon in PWS, 1980-1989.

Stock	Population[a] (N)	Mean wt[b] (kg)	Biomass (kg)
Pink	21,269,184	1.6	34,030,694
Chum	1,632,316	3.6	5,876,338
Total	22,901,500	(1.8)	39,907,032

Based on Morstad et al. (1996, Appendices E.5 & E.9);Weighted mean, based Morstad et al. (1996, Appendix A.5).

functional group.

Adult salmon only feed a short time within PWS; in the model, their low trophic impact can be captured by giving them a low value of Q/B, here 1 year^{-1}, corresponding to 1/12 of the annual value for pink salmon in the Alaska gyre (L. Huato, pers. comm.; Christensen 1996, Table 10). A diet composition (by weight) of pink salmon of 85% small pelagics and 15% macrozooplankton came from Huato (1996).

Table 11. Instantaneous oceanic mortality rates (Z) for five species of salmon occurring in PWS[a].

Species	Total mortality (Z; yr^{-1})
Chinook	0.42
[illegible]	0.92
[illegible]	1.32
[illegible]	2.45
[illegible]	1.64
[illegible]	2.37

a) From Huato (1996), based on Ricker (1975) and Bradford (1995);
b) Weighted by the catches in Table 9.

Miscellaneous small pelagic fishes

This group includes capelin, eulachon, smelt, and other small fishes. While not fished, small pelagics are important in PWS, as they are the major preys of pinnipeds, cetaceans, birds and of many larger fishes.

As no standing stock estimates is available for the small pelagics of PWS, their biomass is left as an unknown to be estimated by the model; given the important role they play in the diet of larger vertebrates, this estimation of biomass will be based on an assumed value of EE = 0.95; the other parameters for this group are set as for the small pelagics of the Strait of Georgia, i.e., P/B = 2 year^{-1} and Q/B = 18 year^{-1} (Venier 1996).

The diet of the small pelagic group (in % weight) is also adapted from that in Venier (1996), with modifications as required to balance the model: mesozoolankton (80); large zooplankton (10); and small macrobenthos (10).

Birds

Of the 219 species of birds recorded in the Northern coast of the Gulf of Alaska and in PWS, 111 are primarily associated with water bodies. A large number of birds concentrate in the PWS area during the Spring migration and smaller numbers during the Fall migration. Shorebirds and waterfowls are especially numerous. During Summer, many nesting species utilizes the PWS area. The most common of these are alcids, black-legged kittiwakes, cormorants, glaucous-winged gulls, and arctic terns. In Winter, waterfowls such as "mallards, greater scaup, common and barrow's goldeneye, buffleheads, oldsquaws, harlequin duck, white-winged -surf -and common scoters, and common and red-breasted mergansers and alcids" use the inshore areas together with many gulls (Isleib and Kessel 1973).

The model of PWS presented here does not consider shorebirds, concentrating instead on seabirds and waterfowls (in that order). Of the latter, only ducks are included, i.e., swans, etc., are not considered.

As mentioned above, many species of ducks overwinter in PWS, while in Summer, scoters are most abundant. Table 12 shows the species composition of ducks wintering in PWS, and Table 13 presents estimates of the abundance of ducks in PWS during summer and winter.

Table 14 summarizes the information on diet composition of ducks in PWS.

The following seabirds are known to breed in PWS, including Montague, Hinchinbrook, and Hawkins Islands (DeGange and Sanger 1986):

- storm petrel (fork-tailed, Leach's);
- cormorants (double-crested, pelagic, red-faced);
- gulls (mew, herring, glaucous-winged, black-legged, kittiwake);
- terns (arctic, Aleutian);
- common murres;
- pigeon guillemot;
- small alcids (kittlitz'a murrelet, parakeet auklet); and

Table 12. Population statistics of ducks overwintering in PWS[a].

Species	Body weight (kg)	Pop. (N)	Biomass (kg)	Food cons.[e] ($kg \cdot year^{-1}$)
Green-winged teal	0.34[b]	rare	-	-
Mallard	1.16	4,600	5,336	389,528
Northern pintail	1.01	50	50.5	3,687
American widgeon	0.76[b]	rare	-	-
Scaup (greater)	1.05	1,400	1,470	107310
Harlequin duck	0.61	4,900	2,989	218,197
Oldsquaw	0.89	1,400	1,246	90,958
Black scoter	1.15	4,850	5,577.5	407,158
Surf scoter	1.10[c]	4,950	5,445	397,485
White-winged scoter	1.35[d]	1,950	2,632.5	192,173
Unidentified scoter	1.15	7,850	9,027.5	659,008
Goldeneyes	0.90	11,600	10,440	762,120
Bufflehead	0.45	1,700	765	83,768
Uniden. merganser	1.12[b]	4,750	5320	388,360
Total	-	50,000[c]	50,299	3,699,752

a) Modified from DeGange and Sanger (1986);
b) From Dunning (1993);
c) From Vermeer (1981, p. 114);
d) From Palmer (1976, p. 115);
e) Consumption was calculated assuming that birds weighing 200-600 g consume 30% of their body weight each day, and birds greater than 600 g consume 20% of their body weight each day (see also Nilsson and Nilsson 1976; Muck and Pauly 1987; and Wada 1996).

Table 13. Estimation of duck biomass in PWS, by season.

Season	Species	Pop. (N)	Body weight (kg)[a]	Density ($t \cdot km^{-2}$)	Cons.[b] ($t \cdot year^{-1}$)	Q/B ($year^{-1}$)
Summer	Scoters	11,000	1.15	0.001	923	73
	Other ducks	11,000	0.90	0.001	723	73
	Total	22,000	-	0.002	1,646	73
Winter[c]	Ducks	50,000	-	0.006	3,700	74
Mean	-	36,000	-	0.004	2673	74

a) Degange and Sanger (1986, Table 16-4);
b) Assuming that the birds eat the equivalent of 20% of their body weight day^{-1} (see Table 12, note e for sources);
a) See Table 12.

Table 14. Diet matrix for some selected ducks in Prince William Sound.

Prey \ pred.	Barrow goldeneyes[a]	Harlequin duck[b]	Old-squaw[c]	Scoter[d]	Mean % in diet
Bivalves	0.712	-	0.6	0.50	0.453
Gastropods	0.096	-	0.2	0.25	0.137
Other molluscs	-	0.434	-	-	0.109
Crustaceans	0.182	0.355	-	0.25	0.197
Insects	-	0.044	-	-	0.011
Echinoderms	-	0.120	-	-	0.030
Sandlance	-	-	0.2	-	0.050
Turbellaria	-	0.005	-	-	0.001
Algae	0.010	0.042	-	-	0.013

a) Modified from Koehl et al. (1982);
b) Modified from Dzinbal and Jarvis (1982);
c) Based on Degange and Sanger (1986);
d) Based on Vermeer and Bourne (1982).

- puffins (tufted, horned).

Other seabirds occurring in PWS are marbled murrelets, red-faced cormorant, pelagic cormorant, double-crested cormorant, common loon, and others (Paine et al. 1996).

Table 15. Seabird densities in PWS. (Modified from DeGange and Sanger 1986).

Season	$N \cdot km^{-2}$
Spring	29.0
Summer	56.7
Fall	35.6
Winter	18.2
Mean	34.9

Table 16. Diet matrix for the seabirds of PWS[a].

Predator \ prey	Cephalopods	Misc. crustaceans	Euphausiids	Decapods	Capelin	Walley pollock	Sand lance	Misc. fishes	Other invertebrates	Sculpins	Shrimps	Pacific sandfish
Fork-tailed storm petrel	0.675		0.223	0.03		0.017		0.042	0.013			
Mew gull[b]		0.067		0.074			0.017	0.035	0.026			
Glaucous-winged gull[b]		0.002	0.004	0.003	0.026		0.016	0.925	0.016			
Black-legged kittiwake	0.001	0.006	0.104	0.002	0.667	0.012	0.086	0.1	0.022			
Arctic tern		0.001	0.968	0.001	0.014		0.013	0.002	0.001			
Aleutian tern		0.022	0.765		0.032		0.12	0.046	0.015			
Pelagic cormorant		0.002		0.004	0.018	0.006	0.858	0.101	0.002	0.009		
Pigeon guillemot[b]		0.013		0.327	0.13			0.399	0.013	0.004	0.051	0.048
Marbled murrelet[b]		0.014	0.053		0.479	0.001	0.213	0.14	0.002		0.001	0.003
Kittlitz's murrelet			0.243		0.018		0.036	0.686				0.017
Parakeet auklet			0.465	0.121				0.414				
Common murre	0.001		0.032	0.01	0.453	0.117	0.239	0.146	0.002			
Horned puffin	0.012	0.002	0.005		0.619	0.001	0.162	0.198	0.001			
Tufted puffin	0.078		0.112		0.741	0.006	0.054	0.007	0.002			

a) Modified from Degange and Sanger (1986). The original diet fractions for the various birds did not all add up to 1. This was corrected for by modifying the fraction contributed by the most important prey groups.
Additional entries not in the table are: mew gulls: 78.1% gammarid amphipods; glaucous-winged gulls: 0.2% hexagrammids, and 0.6% other birds; pigeon guillemot: 1.5% pricklebacks; marbled murrelet: 9.4% mysids.

Of these breeding birds, black-legged kittiwake is the most abundant in PWS, with 20,000 pairs nesting at 27 colonies. They occur in the Sound from February/March to August/September, and feed near the surface, preying chiefly on young herring, Pacific sand lance, capelin and young walleye pollock (Irons 1996).

Pigeon guillemot is another abundant seabird breeding in PWS. It feeds in inshore waters, primarily on benthic fishes and invertebrates. During a survey of the guillemot population in PWS, conducted in 1984 and 1985, 4660 guillemots were counted, compared to 15,000 in 1972-1973 (Oakley and Kuletz 1996).

Table 15 shows rough seabird

density estimates for PWS, by season.

Based on Table 8 in Kelson et al. (1996), the average weight of seabirds is set at 0.5 kg, resulting in an overall density of 0.017 t·km^{-2} over PWS.

Assuming, with DeGange and Sanger (1986), that seabirds between 200 and 600g consume about 30% of their body weight per day, leads to an estimated total food consumption of 2.157 tonnes annually, corresponding to a Q/B estimate of 110 year^{-1}. The diet matrix, indicating the food items thus consumed, is given as Table 16.

The summary statistics used for the combination of waterfowls and seabirds are: biomass = 0.021 t·km^{-2} (see Tables 13 and 15); P/B = 0.1 year^{-1} (from Muck and Pauly 1987); and Q/B = 103 (weighted mean, given 88 % seabirds and 12 % ducks). The mean (weighted) diet composition derived from Tables 14 and 16 for this combined group, is: pelagic fish, including cephalopods (45.9 %); invertebrates (21.5%); demersal fish (13.6%); euphausiids (18.7%) algae (0.2%); and insects (0.1%).

Sea otters

Two estimates of the population size of sea otters in PWS exist for the period considered here: 4000-6000 in 1985, and 5000-10,000 in 1989 (Burn 1994). The mean of the midranges, multiplied with the mean weight of adults (females 21, males 28 kg; Calkins 1986) and assuming a female male ratio of 1:1, leads to a density of 0.017 t·km^{-2} for PWS as a whole.

Further, given daily rations of 5.3 kg for the females and 7.0 kg for the males (Calkins 1986), Q/B is estimated as 92 year^{-1}. The major prey organisms of sea otters in PWS are mollusks, crustaceans, and echinoderms (Garshelis et al. 1986, Calkins 1978); Table 17 summarizes the results of an analysis of the diet composition of sea otters in Montague Strait.

Table 17. Diet composition of sea otters in Montague Strait, PWS (adapted from Calkins 1976 and Garshelis et al. 1986).

Food item	Contrib. (% wt.)
Molluscs	
clams	81.0
mussels	0.3
octopus	0.6
Crustaceans	-
crabs	7.0
Echinoderms	-
seastar	0.9
sea cucumber	0.3
Others inverts	9.9

Other marine mammals

The marine mammals of PWS, besides sea otters, can be split into three groups: resident, transient, and pinnipeds. The first group comprises killer whales, Dall's porpoise, and harbor porpoise. The second group comprises fin whales, humpback whales, minke whales, beluga whales, and killer whales, occurring only seasonally in PWS. The third group is comprised of harbor seals and Steller sea lions. Table 18 summarizes key population statistics of the different species. Note that in this table, the Q/B values are based on sex ratios of 1:1, except for Steller sea lion, where there are 1.2 females per male (Calkins 1986).