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Hecate Strait Project Report on the Hecate Strait Ecosystem Modelling Workshop

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HECATE STRAIT PROJECT

REPORT ON THE HECATE STRAIT ECOSYSTEM MODELLING WORKSHOP

by

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ABSTRACT

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A workshop was convened to develop hypotheses and models that might explain fluctuations in the time series of abundance of various species in the area of Hecate Strait. The conceptual basis for two models was synthesized. In one model, Pacific cod and Pacific herring time trends were approached as though they might be explained by the feeding of cod on herring and other species. In a second model, the trends were approached as though they might be explained by physical oceanographic phenomena.

RESUME

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Un atelier a été tenu afin d'élaborer des hypothèses et des modèles permettant d'expliquer les fluctuations des séries chronologiques de l'abondance de diverses espèces se trouvant dans les environs du détroit d'Hécate. Les concepts de deux modèles ont été déterminés. Dans l'un des modèles, les tendances temporelles de la morue et du hareng du Pacifique sont traitées comme pouvant s'expliquer par la prédation du hareng et d'autres espèces par la morue. Dans le second modèle, les tendances sont traitées comme pouvant s'expliquer par des phénomènes océanographiques physiques.

INTRODUCTION

During planning meetings for the Hecate Strait Project of the Fisheries Research Branch (Department of Fisheries and Oceans, Pacific Region) in the spring of 1983, the planning group decided to have a systems modelling workshop. The general purpose of the workshop was to formalize some of the ideas being developed for an increased understanding of productivity relationships in the Hecate Strait region. The project coordinator (A. V. Tyler) subsequently discussed with C. J. Walters and R. Hilborn the possibilities of holding the workshop at the Institute of Animal Resource Ecology, University of British Columbia. The workshop was held in two sessions. The first session was a four-day period in late January, 1984; the second was a one-day wrap-up session on March 1, 1984. The modelling workshop was led by C. J. Walters and R. Hilborn, with the following participants from the Pacific Biological Station during the four-day session: T. Butler, A. Dodimead, M. Healey, M. Saunders, M. Stocker, L. Richards, A. Tyler, and S. J. Westrheim. Invited guests present were P. LaBlond, M. LaBelle, and W. Crawford (Fig. 1). M. LaPoint was helpful in discussions, and in entering data into the computer. The one-day finale was attended by a large group of interested scientists.

OBJECTIVES AND ORGANIZATION

The approach taken during the modelling session was to develop a system dynamics framework for aspects of productivity in Hecate Strait. The group examined possibilities for mixed species assessment and management, identified information gaps that would mitigate against an understanding of the dynamics of economically important species in the area, and formalized hypotheses about the natural productivity of those species that would later become focal points for research in the Hecate Strait Project. In a sense, the group developed statements of the "best-guess" understanding of selected aspects of natural production of the region; a statement that would serve as a strawman for the group to kick at during the five-year duration of the project. The intention was that the models would undergo modification as research proceeds, so that later versions would be a better representation of the natural production system than could be formed at the time.

Some of the general hypotheses that the group had formalized prior to the workshop were:

1. Herring (<u>Clupea harengus pallasi</u>) and sandlance (<u>Ammodytes hexapterus</u>) have a central role as food-energy converters for other species of economic interest.

2. Herring stock dynamics can not be understood without some information on their predators.

3. Dungeness crab (<u>Cancer magister</u>) are strongly linked to groundfish productivity because they share food resources with soles and are eaten by several species of groundfish.

4. Dogfish (Squalus acanthias), halibut (Hippoglossus stenolepis), juvenile sablefish (Anoplopoma fimbria), and first-sea-year salmon species have a strong predatory impact on other economically important species in Hecate Strait.

5. Physical oceanographic events are important in setting recruitment patterns for Pacific cod (Gadus macrocephalus), rock sole (Lepidopsetta bilineata), and Pacific herring.

Participants divided themselves into four working groups. One group developed a model of recruitment in relation to physical factors, and a second group developed a predator-prey model that might explain stock trends. The main effort during the modelling session was to construct the model concepts rather than carry out a complete computerization and analysis, though some computer entry was done. Each group developed functional relationships between organism responses and independent variables, and developed the model logic. Computer models were completed after the sessions of the workshop, and will be published at a later date.

MODEL FOR RECRUITMENT IN RELATION TO PHYSICAL FACTORS

The purpose of this model was to estimate the survival of eggs and larvae of Dungeness crab, Pacific cod, and Pacific herring based on hypothetical relationships between survival rates and physical oceanographic factors. Four factors were incorporated into the model: (1) the influence of temperature on egg hatch; (2) the influence of temperature on larval survival; (3) the influence of wind-driven water mass advection on larval retention; (4) the influence of high temperature anomalies in forcing juveniles away from shallow, protective habitat into deeper water where they would be exposed to heavier predation from large piscivores.

Percentage hatch of the liberated eggs for herring and Pacific cod was based on laboratory work (Alderdice and Velsen 1971; Alderdice and Forrester 1971). This work showed that salinity had a strong influence on hatching, and that at the relatively high salinities prevailing in Hecate Strait ($\approx 30°/_{\circ\circ}$), percentage hatch is substantially reduced for both species. However, there is doubt as to whether this depression in percentage hatch would actually occur in the natural environment, since these fishes tend to be found naturally at high salinities rather than at low salinities (Alderdice, pers. comm.). Because of this, we set two hypotheses for each species; one for the case in which salinity decreases percentage hatch, and one in which it does not. For both species a dome-shaped curve is likely (Fig. 2). The temperature series to be used was McGinness Island lighthouse in February for Pacific cod, and in May for Pacific herring.

There is evidence that water advection influences survival rates of larval fish (Kruse 1984). We used a transport index calculated from daily atmospheric pressure maps by A. Bakun (1973), and updates to 1981 with a computer file, at a point 51° N lat. 131° W long. which is just offshore of Queen Charlotte Sound, moving water to the north in Queen Charlotte Sound and Hecate Strait. Our opinion was that, under the most favorable (low) transport levels, a baseline mortality through the larval stages would be about 80%, and that this could reach 99% if transport to the north was very high, nearly flushing the Strait (Fig. 3). The transport series used was January, plus February, and March for cod, and May for herring. Transport mortality was not added to Dungeness crab, because the winds are lighter in the early summer when the hatched crabs are in the plankton.

Crab larval mortality was incorporated into the model via an inverse linear relationship between percentage annual mortality and mean July temperature (Fig. 3). This hypothesis was based on laboratory work (Prentiss 1971).

Cod and herring larvae are assumed to graduate to the juvenile stage by April for cod and by the end of May for herring. We developed the hypothesis that the juveniles are displaced from their shallow and protective habitat to deeper water in warmer summers, and that they are subjected to increased predation from large piscivorous fishes when they are displaced. This hypothesis is based on information on distribution of fish by size, larger sizes (predators) being in deeper water. It is also based on observations (Fargo, pers. comm.) that, in warmer summers, the distribution of juveniles is shifted from shallow to deeper water in relation to the depth of the bottom of the thermocline. As the warmer water of the upper layer penetrates deeper, the fish move to the deeper, cooler water. The relationship between availability to predation by predator j, α_j, and the summer temperature anomaly (Fig. 4) is conceived as a direct linear one with positive anomalies in the summer (June through September).

The predation mortality actually occurs in the multi-species disk equation in that sub-model. This is effected by multiplying α_j by the vulnerability factor, v_{ij}, where v_{ij} is described in the next section.

MODEL FOR STOCK TRENDS IN RELATION TO PREDATION

This model describes predation rates on Dungeness crab, Pacific cod and Pacific herring by the known predators for which historical abundances could be reconstructed (sablefish, dogfish, salmon, halibut). We chose the multi-species disc equation (Murdoch 1973) as the basic approach because the equation can be derived from basic assumptions of predator time budgets and the parameters can be determined experimentally. It also allows a high degree of flexibility (Fig. 5).

The annual survival rate from predation for a prey i is $e_j^{-\Sigma_j m_{ij}}$. Here, the summation is over j predators. The instantaneous mortality rate is $m_{ij} = c_{ij}N_j/N_i$ where c_{ij} is the number of prey i eaten by predator j in a year (one time unit), and N_i and N_j are the prey and predator abundances.

Then, from the disc equation

$$c_{ij} = \frac{a_j v_{ij} N_i}{B_j + a_j \Sigma_k v_{kj} N_k / m_{kj}}$$

where

a_j is the rate of effective search for predator j
v_{ij} is the relative vulnerability of prey i to predator j
m_{kj} is the maximum possible number of type k prey eaten in a year by predator j.
B_j is a term to account for the time spent handling prey types not explicitly included in the model. If all prey types are included then B_j=1.

The rate of effective search, a_j, is the product of the distance searched by predator j in one year, twice the reaction distance, and the proportion of time spent feeding, divided by the area of Hecate Strait (1500 km^2). This parameter has units of the number of Hecate Straits searched per year. The distance searched can be estimated by assuming a swimming speed of one cm/sec for each body length, or 316 km/yr/cm body length. The proportion of time spent feeding is assumed to be 0.40. Reaction distance was set as a best guess at 10^{-5} km for herring, and 10^{-4} km for cod, rock sole, and sablefish.

The vulnerability of prey i to predator j, v_{ij}, is the encounter probability times the probability of capture given that an encounter has occurred. It can be estimated relative to type 1 prey as

$$(c_{ij}/c_{1j})\cdot(N_1/N_i)$$

This is the proportion by number of prey i in the diet of predator j relative to a dominant prey type, corrected by the ratio of the abundances of those prey types. The model requires c_{ij} and c_{1j} as inputs and determines v_{ij} from calculations of the annual abundances.

B_j is given by

$$B_j = \frac{a_j w_1 N_1 (1-K_j)}{P1j\, W_j K_j}$$

where w_1 is the weight of type 1 prey

P1j is the proportion by weight of type 1 prey in the diet of predator j

K_j is a measure of average gut fullness, assumed to be 0.5

and

W_j is the maximum weight of prey consumed per year, estimated as three times the annual weight increment for the predator.

The value of B_j is most susceptible to error when the prey types included in the model comprise only a small portion of the diet of the predator. Sandlance, for example, is a major food item that is not treated explicitly. To test for an interaction between the abundances of sandlance and another prey species, B_j could be replaced by some function of sandlance abundance. Similarly, B_j could be replaced by a function of environmental variables to test the hypotheses that food abundance fluctuates with, for example, temperature.

The main parameters that must be estimated for each predator are the rate of effective search and the average weight of food consumed. Prey weight and the proportion by number of each prey type in the predator diet are also required. Initial estimates that we derived for these parameters are listed in Table 1.

The proportion by number is difficult to estimate as stomach content data are generally recorded by weight rather than by number. An alternative approach however, is to estimate an average value and/or an upper limit to the number of each prey type eaten per predator in a year. The proportion by number can then be back calculated from these data. For example, consider adult Pacific cod feeding on herring. From gut contents data there are 6 to 8 herring per cod stomach over the period January to March, when the populations overlap (Westrheim, pers. obs.). Assuming that cod feed at 2-day intervals, and that the stomachs are 50% full, then each cod consumes approximately 160 herring in one year. Estimates derived in this manner are listed in Table 2 along with initial prey and predator abundances.

MODELLING PREDATION BETWEEN COD AND HERRING

We noticed during the workshop that there was a strong inverse relationship between cod and herring stocks in Hecate Strait (Fig. 6; Table 3). The relationship was not so strong in areas to the south, indicating that factors influencing the species in the Strait were unique for the Canadian Pacific coast. We proposed the hypothesis that a predator-prey cycle existed in the Strait that was obscured by physical oceanographic factors in more southerly areas where cod were at the extreme southern end of their range. Regression analyses of herring juvenile survival as measured by log recruits per herring spawner on Pacific cod abundance (r=0.41, d.f.=19, significant at p=0.1) indicate that the cod may cause a total instantaneous mortality rate averaging around 0.75 yr^{-1} with each cod consuming several hundred herring. Somewhat lower estimates of herring consumption per cod were expected on the basis of stomach contents data, but the discrepancy may well be due to sampling problems. Cod recruitment rates are positively correlated with herring abundance (r=0.48, d.f.=19, significant at p=0.1), but it is impossible to determine from historical data whether this correlation reflects predator-prey interdependence or the impacts of older cod on their own offspring, since cod and herring abundances are inversely correlated. Peak cod abundances during the late 1950s may be partly responsible for the collapse of the herring reduction fishery of the 1960s, and management of the two species should be coordinated to reflect the possiblity of similar events in the future.

The herring-cod relationship will be developed further as a research study of the Hecate Strait Project. Other time-series that were considered during the workshop are given in Table 4.

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Table 1. Prey weight and the average proportion by number for each prey type in the predator diet. Parameter estimates for the predators are also given. Units for a_j are km^2/year times 10^{-4}. Headings L, J, and A refer to larvae, juveniles, and adults, respectively.

				Prey types						
				Herring			Crab			Cod
				L	J	A	L	J	A	L
Prey weight (g)				8	46	84	0.5	200	700	8×10^{-5}
Predators		a_j	W_j							
Herring	J	0.1	90	.1						
	A	0.2	60							.08
Crab	J	0.5	450					.02		
Cod	J	0.5	15000							.01
	A	0.1	2400			.05				
Sablefish	J	0.7	750		.3	.1				
Dogfish	A	3.0	330		.01	.05		.001		
Salmon	J	5.0	2400		.01					
	A	10.0	6000		.01	.005	.1			
Halibut	A	2.0	5400					.06	.03	

Table 2. The average number of prey consumed for each predator in a year, the maximum possible number consumed in a year, and initial predator and prey abundances. Units for abundance estimates are 10^6.

Predator		Prey		Mean prey eaten per predator	Maximum prey eaten per predator	Number predator	Number prey
Herring	J	Herring	L		1.	4400	5.3×10^6
Herring	A	Cod	L		96.0	2600	1900
Crab	J	Crab	J	1.2		7	7
Cod	J	Cod	L	3000.0		6	1900
Cod	A	Herring	A	160.0	1.4	2	2600
Sablefish	J	Herring	J	4.1		18000	4400
Sablefish	J	Herring	A	0.41		18000	2600
Dogfish	A	Herring	J	2.5	64.0	18	4400
Dogfish	A	Herring	A	4.0	117.0	18	2600
Dogfish	A	Crab	J	0.4	27.0	18	7
Salmon	J	Herring	J		24.0	190	4400
Salmon	A	Herring	J		21.0	5	4400
Salmon	A	Herring	A	-	3.0	5	2600
Salmon	A	Crab	L	5.4×10^{-4}	640.0	5	4900
Halibut	A	Crab	J	5.6		1	7
Halibut	A	Crab	A	0.4		1	6

Table 3. Stock and recruitment data assumed for cod and herring. Herring effective egg deposition E_t was taken as column (1) x 2000. Cod effective egg deposition E_t was taken as column (3) x 1000. All numbers are millions of fish.

Year	Herring adult ($\geq$ age-3) stock size (1)	Herring age-1 recruits, year of birth (2)	Cod adult ($\geq$ age-3) stock size (3)	Cod age-1 recruits, year of birth (4)
1955	2640	3590	1.9	2.1
1956	1720	5860	1.1	4.3
1957	1820	1820	1.9	4.3
1958	3120	7560	3.7	2.1
1959	2140	6270	3.7	2.8
1960	4070	5140	1.9	4.3
1961	4350	9680	1.8	6.9
1962	4210	3550	2.5	7.8
1963	5610	1280	3.8	4.4
1964	4030	670	6.0	3.2
1965	2320	1970	6.6	4.2
1966	1170	2140	5.1	1.4
1967	1050	2700	3.0	1.7
1968	1470	3430	2.6	2.4
1969	2030	3290	1.5	3.1
1970	2650	6080	1.3	4.6
1971	2940	4440	2.1	3.4
1972	4240	5500	3.0	4.0
1973	4370	1690	3.9	3.3
1974	4890	2540	3.3	3.1
1975	3670	2100	3.0	3.4

Table 4. Hecate Strait biological data series. The data listed in this table represent rough estimates of annual values for a variety of species presented at the workshop as approximations for the purposes of conceptual modelling. These data should not be used in circumstances where true values are needed, for example, for stock assessments and catch quota setting. Sources of data are as follows: Crab, T. H. Butler; soles, J. Fargo; sandlance, S. J. Westrheim; salmon, M. C. Healey; sablefish, G. A. McFarlane; dogfish, M. Saunders; halibut, IPHC Sci. Rept. No. 67 1983, Table 1 and Table 4.

Year	Crab catch (thou. kg)	Crab fishing effort (d)	Rock[a] sole year-class strength (thousand females at age-4)	Total rock sole stock (thousand of fish)	English[a] sole yr-class strength thousand females at age-4	Halibut Area 2 stock size (thous. of lbs)	Halibut % of Area 2 stock in B.C.	Sand-lance (stock size numbers in 10^9)
1955	1,0641,178	732	1954	2912	1809	193	.59	25
1956	612,824	409	1060	2123	1809	173	.59	2
1957	623,577	356	564	3752	1871	154	.58	35
1958	1,338,048	468	551	4490	1441	158	.59	32
1959	1,261,771	493	1049	4993	995	176	.60	18
1960	1,267,543	373	1920	5202	1358	179	.60	28
1961	1,091,767	492	1941	4225	1648	163	.60	35
1962	456,147	533	1919	3334	2040	166	.60	18
1963	527,860	498	1480	3385	3353	168	.60	25
1964	1,033,486	670	1228	4097	1393	142	.59	25
1965	437,814	451	1113	4925	784	137	.59	35
1966	754,764	398	476	5896	652	134	.58	35
1967	1,190,244	691	294	4662	982	130	.58	35
1968	933,202	519	371	4132	1303	119	.58	35
1969	658,979	484	803	3168	1577	122	.57	35
1970	552,158	338	878	2323	1647	105	.57	14
1971	239,724	175	514	1792	1949	114	.58	28
1972	10,266	31	638	1130	1674	94	.59	21
1973	30,391	71	678	1523	1086	114	.60	14
1974	50,548	51	1418	2040	846	114	.61	25
1975	177,808	275	1500	2039	636	107	.62	35

Table 4 (cont'd)

Year	Sablefish[a] 4-yr-olds year-class strength (thousand of fish)	Dogfish (stock size thousand of tonnes)	Index of adult abundance - catch in pieces x 10^5				
			Chinook	Sockeye	Coho	Pink	Chum
1955	4000	72	0.65	2.85	3.73	27.47	1.57
1956	4000	73	0.54	2.63	4.59	28.75	2.39
1957	4000	75	0.49	3.37	3.62	27.73	3.80
1958	4000	72	0.73	8.01	3.13	28.85	4.26
1959	4000	71	0.73	3.13	2.61	11.22	0.70
1960	4000	68	0.81	2.92	2.99	16.35	1.86
1961	4000	71	0.53	10.59	3.51	30.61	2.43
1962	4000	75	0.75	6.88	5.87	77.83	4.02
1963	4000	77	1.14	3.03	6.84	28.13	3.91
1964	2795	81	1.43	10.49	8.66	42.76	9.45
1965	3727	84	1.41	5.08	7.27	18.01	3.00
1966	2902	88	1.44	7.88	10.21	76.66	5.55
1967	2421	92	1.41	11.68	3.22	5.94	5.16
1968	2026	97	1.58	9.29	9.40	57.49	11.04
1969	1711	102	1.39	6.20	2.33	5.86	1.50
1970	1603	106	1.29	7.69	5.07	61.36	7.55
1971	1420	112	1.52	9.51	3.62	13.53	4.41
1972	1424	112	2.24	8.42	7.47	77.72	9.45
1973	1070	117	1.53	13.88	3.64	11.63	6.98
1974	1022	122	1.65	14.58	3.28	12.52	3.95
1975	1017	128	1.50	5.40	1.66	9.21	0.53

Table 4 (cont'd)

Year	Index of juvenile abundance[b]				
	Sockeye	Chinook	Coho	Chum	Pink
1955	27.6	5.0	81.9	71.8	8.3
1956	23.9	6.6	106.8	17.5	9.2
1957	5.8	6.4	90.6	25.6	7.8
1958	16.6	9.0	93.1	50.0	8.8
1959	24.1	6.9	109.5	61.2	10.0
1960	31.6	7.5	145.2	9.2	17.1
1961	29.0	4.3	102.0	45.4	5.7
1962	12.8	4.9	154.8	40.6	4.2
1963	37.1	7.4	370.0	82.5	7.7
1964	23.8	5.5	195.4	54.0	8.7
1965	39.5	7.5	244.2	90.4	6.4
1966	30.3	9.5	148.7	46.8	5.3
1967	23.5	8.9	190.8	97.6	8.8
1968	21.0	10.3	58.6	81.1	7.4
1969	23.7	5.4	293.8	88.8	6.4
1970	27.0	7.6	81.5	36.0	5.7
1971	30.7	5.1	197.9	40.2	5.3
1972	32.2	5.9	121.9	42.8	6.5
1973	36.3	3.7	286.0	64.2	5.2
1974	28.4	4.8	118.2	68.6	8.2
1975	34.1	3.5	112.8	56.5	6.6

[a]year-class strength given on year of birth.

[b]Estimated number in millions entering Hecate Strait = escapement x 1/2 x young/female, where sockeye = 75 smolts/♀, coho = 50 smolts/♀, pink = 150 fry/♀, chum = 250 fry/♀, chinook = 300 smolts/♀.

PARTICIPATION OF INDIVIDUALS IN THE WORKSHOP

Workshop Organization and Conduct

R. Hilborn

A.V. Tyler

C.J. Walters

Development of Physical Factor Model

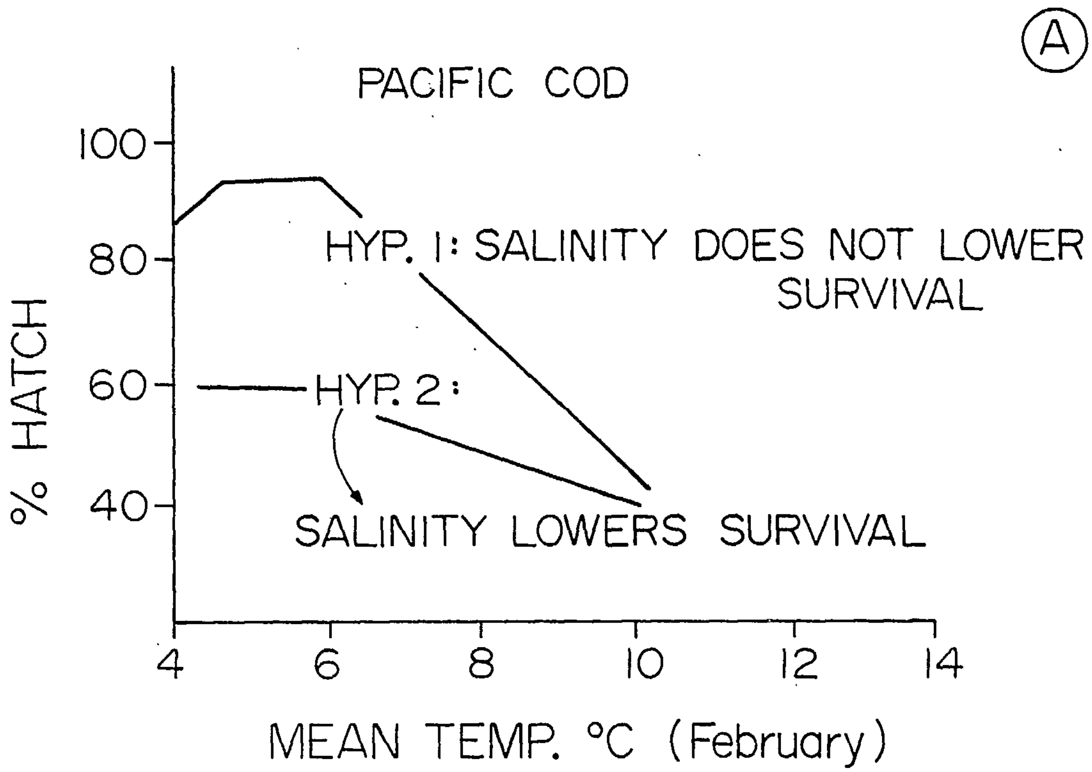
T. Butler	P. LaBlond
W. Crawford	M. Stocker
A.J. Dodimead	A.V. Tyler
R. Hilborn	

Development of Predator-Prey Model

M. Healey	M. Saunders
M. LaBelle	C.J. Walters
M. LaPoint	S.J. Westrheim
L.J. Richards	

Fig. 1. Participants at the workshop and their roles.

Fig. 2. Relationship between percent hatch and surface temperature during the month when eggs are hatching. The salinity in Hecate Strait is higher than salinity for optimum survival seen in laboratory experiments. Hypothesis 1 gives change in optimum survival with temperature. Hypothesis 2 gives the lower survival rates possible at higher salinities according to the laboratory work. Panel A is for Pacific cod, and panel B is for Pacific herring.


A
PACIFIC COD
100
80
60
40
% HATCH
HYP. 1: SALINITY DOES NOT LOWER SURVIVAL
HYP. 2:
SALINITY LOWERS SURVIVAL
4
6
8
10
12
14
MEAN TEMP. °C (February)

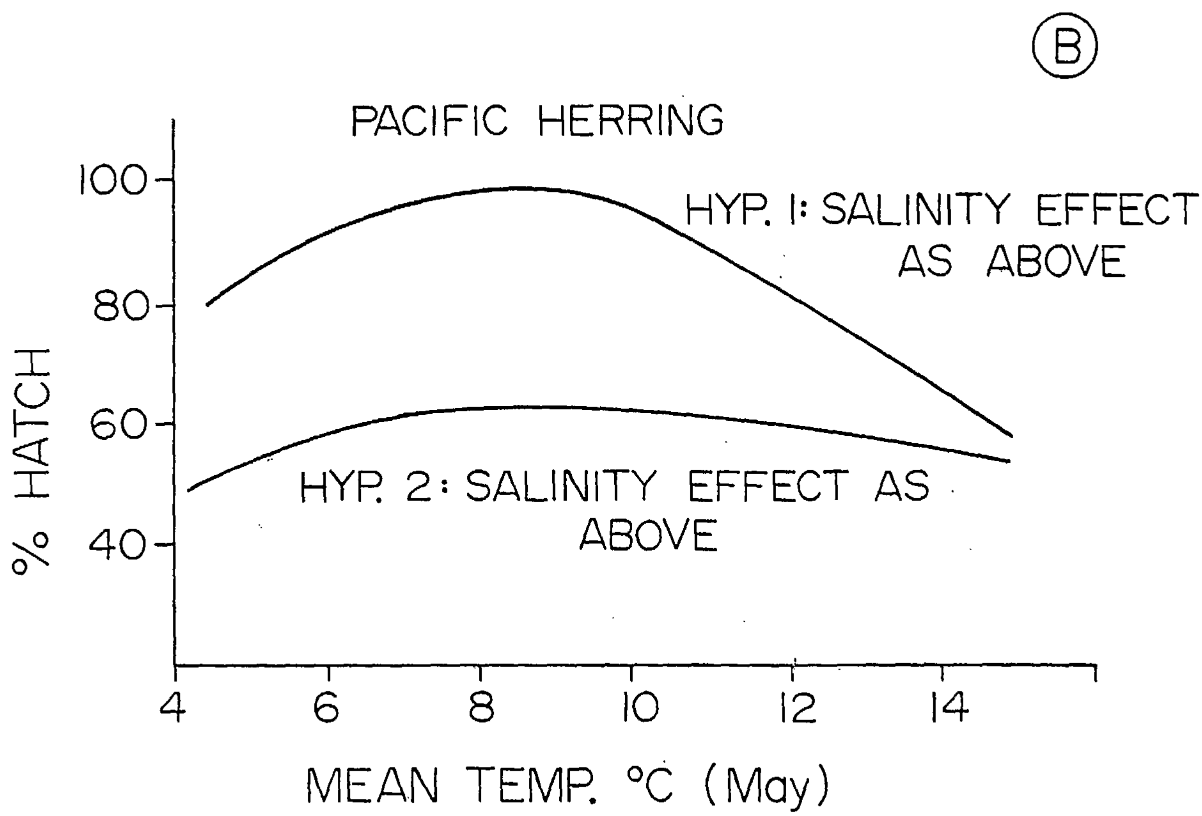
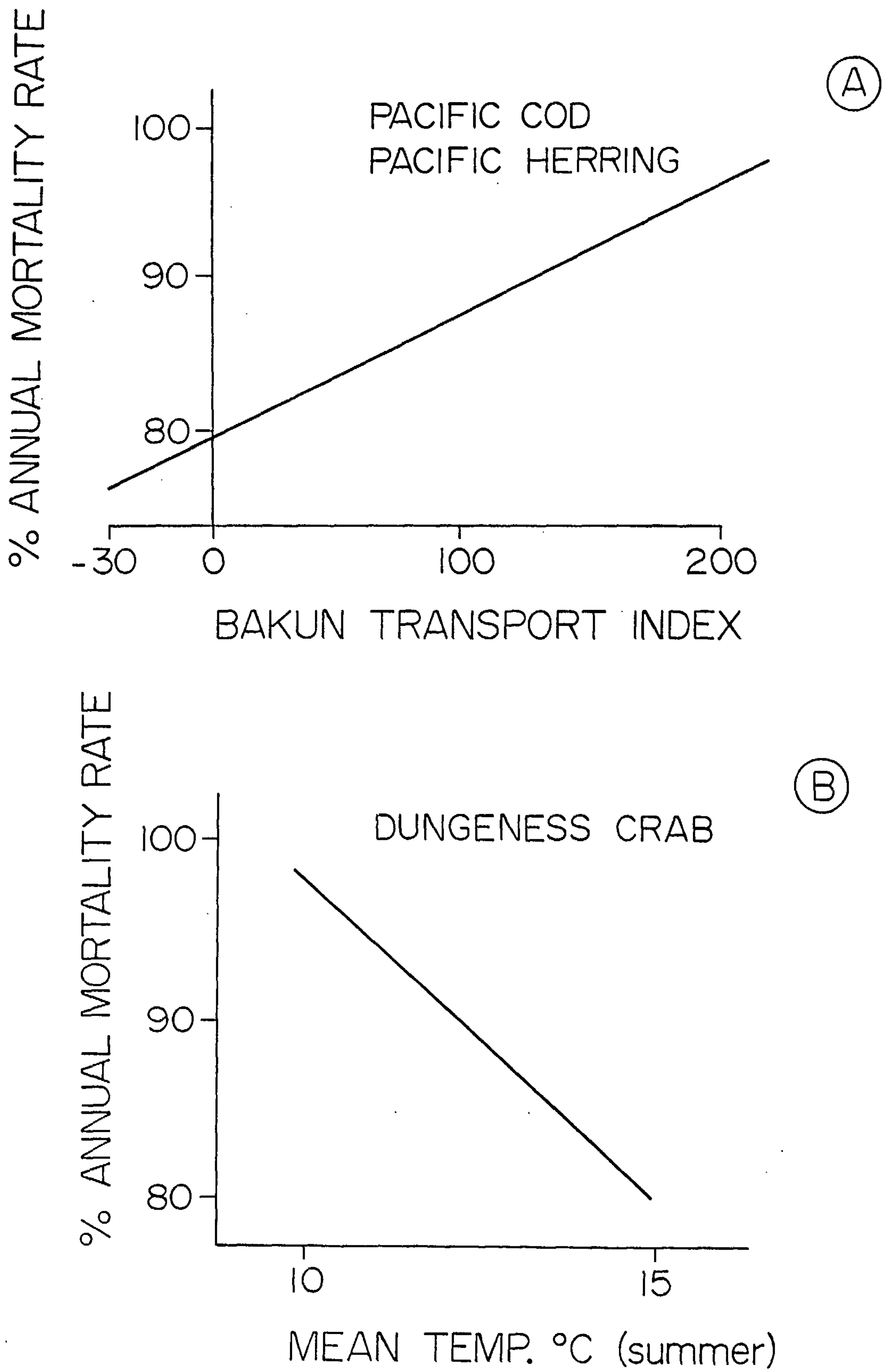

B
PACIFIC HERRING
100
80
60
40
% HATCH
HYP. 1: SALINITY EFFECT AS ABOVE
HYP. 2: SALINITY EFFECT AS ABOVE
4
6
8
10
12
14
MEAN TEMP. °C (May)

Fig. 3. Panel 3A shows the hypothetical relationship between annual percentage mortality rate and northward transport in Hecate Strait (Bakun's index based on the wind force field). The annual historic series used was the February Bakun index for Pacific cod, and the May index for Pacific herring. Panel 3B is relationship between annual mortality rate and summer (June through September) surface temperature for Dungeness crab larvae.



% ANNUAL MORTALITY RATE
A
PACIFIC COD
PACIFIC HERRING
100
90
80
-30
0
100
200
BAKUN TRANSPORT INDEX
% ANNUAL MORTALITY RATE
B
DUNGENESS CRAB
100
90
80
10
15
MEAN TEMP. °C (summer)

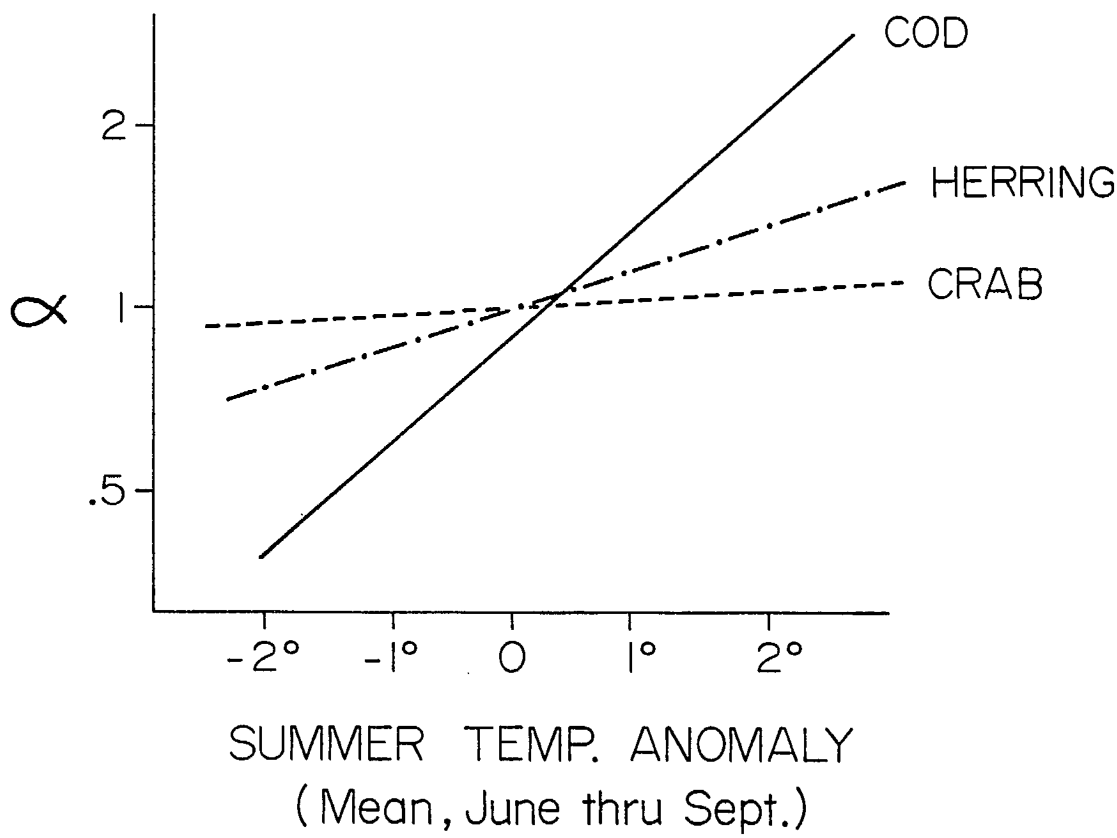


Fig. 4. Relationship between the proportional availability index (t) and summer surface temperature anomalies in Hecate Strait for cod, herring, and crab. Lower than average temperature anomalies bring about reduced exposure to predation. Cod hypothetically are more sensitive to the effects of temperature than are herring and crab.

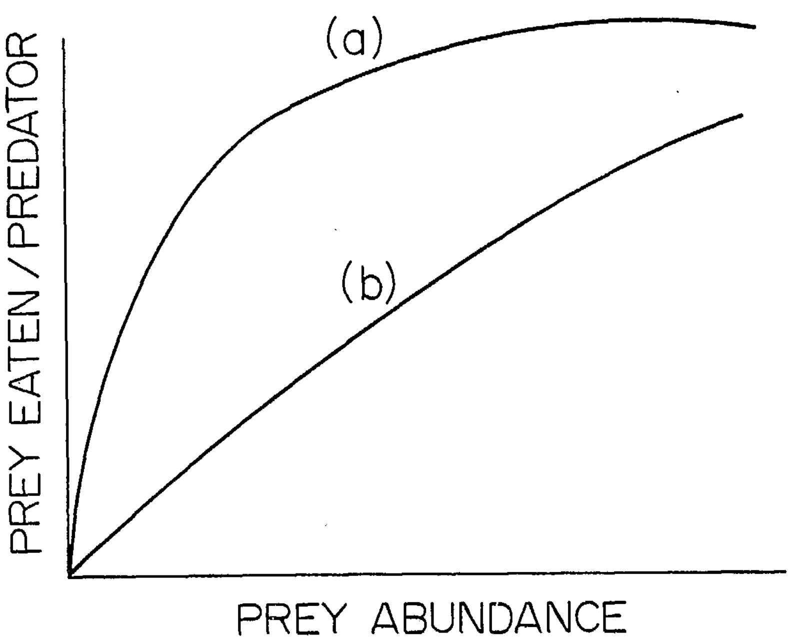
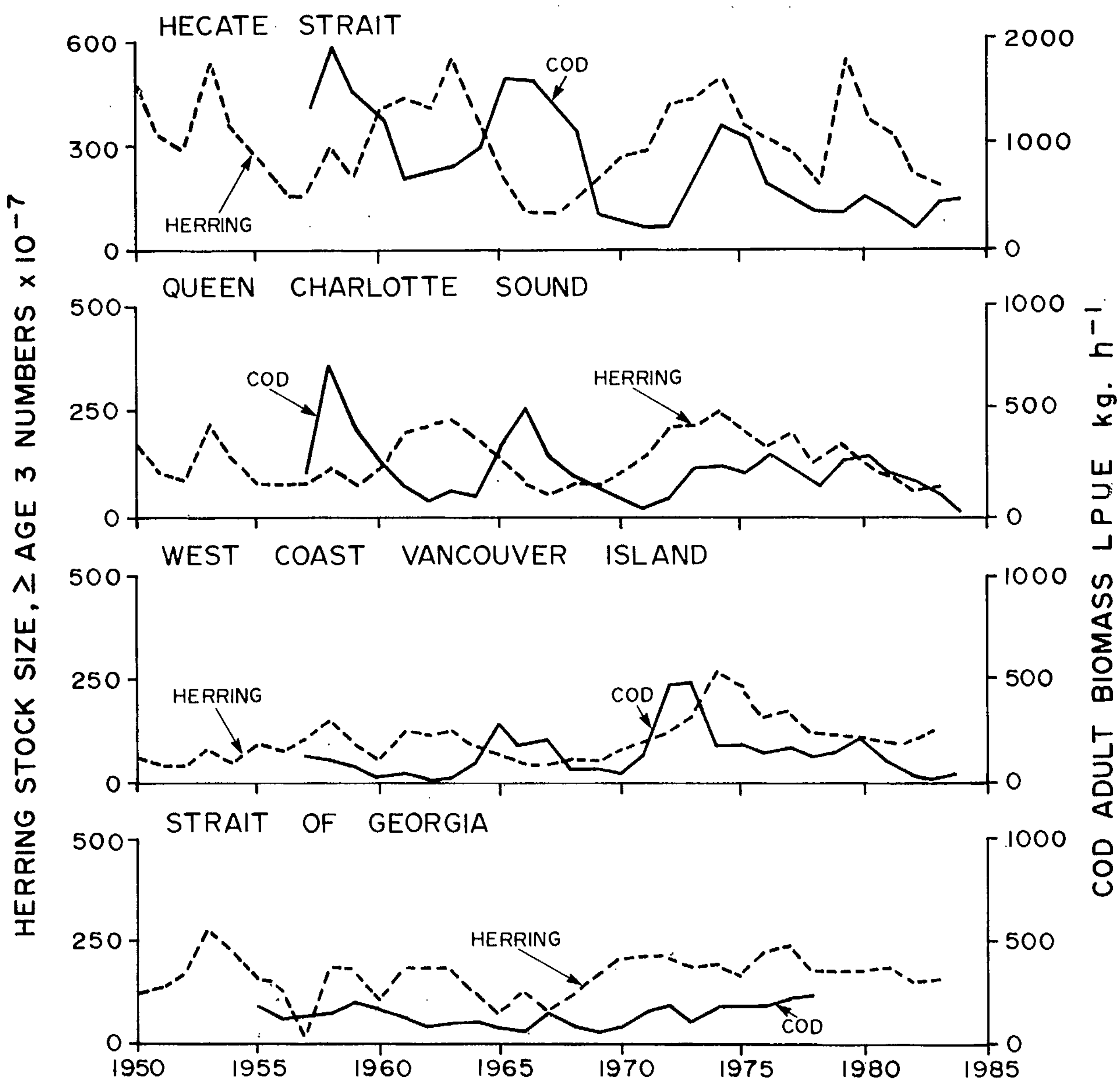


Fig. 5. Two forms of the multi-species disc equation. In (a), search efficiency is high so that predators quickly become satiated. In (b), the number of prey consumed per predator is roughly proportional to prey abundance over the range of prey abundances that normally occur.

Fig. 6. Estimates of adult herring stock size compared to adult cod stock size (landings per unit effort) for various regions of the B.C. coast, from data in Haist and Stocker (1984) and Westrheim and Foucher (1985). Cod catch regions are as named. Hecate Strait (Areas 5C-D) herring include Queen Charlottes and North Coast stocks, Queen Charlotte Sound (Areas 5A-B) herring are central coast stock, west coast Vancouver Island (Areas 3C-D) and Georgia Strait plus Johnstone Strait (Area 4B) stocks are as reported in Haist and Stocker (1984).


HECATE STRAIT
QUEEN CHARLOTTE SOUND
WEST COAST VANCOUVER ISLAND
STRAIT OF GEORGIA
COD
HERRING
HERRING STOCK SIZE, ≥ AGE 3 NUMBERS x 10^-7
COD ADULT BIOMASS LPUE kg. h^-1
600
300
0
2000
1000
500
250
1000
1950
1955
1960
1965
1970
1975
1980
1985