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Metapopulation dynamics of British Columbia herring during cool and warm climate regimes

Dynamique de la métapopulation de hareng de la Colombie-Britannique pendant des régimes de temps chaud et de temps froid

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ABSTRACT

In a previous paper (Ware and Schweigert 2001) we documented the dispersal and production dynamics of the five major BC herring stocks during the recent 1977-98 “warm” climate regime, and incorporated the results into a structured metapopulation model (SMP). In this paper we analyze the dispersal and production dynamics of the five major BC herring stocks during the 1951-76 “cool” climate regime, and include the results in the SMP model to estimate dispersal during this period. We also compare and contrast the dispersal rates and production dynamics of the major BC herring stocks during the complete time series (1951-98). The dispersal rate appears to be density-dependent during both climate regimes. Consequently, dispersal tended to be higher during the warm regime, because the average biomass of spawners was larger. Recruitment to the Queen Charlotte Islands (QCI) and West Coast of Vancouver Island populations was significantly reduced during the warm regime, and decreased the productivity of these populations. The dispersal rate time series output by the metapopulation model imply that the Georgia Strait and Prince Rupert populations tend to be significant exporters of adult herring to other populations, while the Central Coast and QCI populations tend to be major importers. The appearance of a large year-class in one of the local populations will set up a dispersal wave, which radiates throughout the metapopulation until it is depleted by natural and fishing mortality. The dispersal rate time series indicate that seven, large dispersal waves probably occurred since 1951. Dispersal is an important process because it tends to stabilize the spatial distribution of spawners in the metapopulation, and increases the persistence time of the less productive, local populations in two ways: 1) the density-dependent dispersal response increases the fidelity rate when a population is declining, and (2) declining populations will tend to receive more migrants from other populations than they export. Dispersal is also important because it recolonizes new (or vacant) spawning habitat. This enables the metapopulation to adapt to habitat changes, and to alter its spatial distribution in response to low frequency trends in climate, and other factors.

RÉSUMÉ

Dans une étude précédente (Ware et Schweigert, 2001), nous avons documenté la dynamique de la dispersion et de la production chez les cinq principaux stocks de hareng de la Colombie-Britannique pendant le récent régime de climat « chaud » prévalant de 1977 à 1998 et intégré les résultats dans un modèle de métapopulation structurée (MPS-SMP). Dans le présent document, nous analysons la dynamique de la dispersion et de la production des cinq principaux stocks de hareng de la province pendant le régime de climat « froid » prévalant de 1951 à 1976 et intégrons les résultats dans le modèle de MPS en vue d'estimer la dispersion pendant cette période. Nous comparons ensuite les taux de dispersion et la dynamique de la production chez ces cinq stocks pendant toute la série chronologique (1951-1998). Comme il semble que le taux de dispersion est dépendant à la densité pendant les deux régimes climatiques, la dispersion avait tendance à être plus forte pendant le régime de temps chaud parce que la biomasse moyenne de reproducteurs était plus élevée. Le recrutement aux populations des îles de la Reine-Charlotte et de la côte ouest de l'île de Vancouver était nettement réduit pendant le régime de temps chaud, ce qui a donné lieu à une baisse de productivité de ces populations. La série chronologique de taux de dispersion issue du modèle de métapopulation laisse supposer que les populations du détroit de Georgia et de Prince Rupert ont tendance à alimenter d'autres populations en hareng adulte, tandis que les populations de la côte centrale et des îles de la Reine-Charlotte ont tendance à être alimentées de la sorte. L'avènement d'une abondante classe d'âge dans une des populations locales entraînera une vague de dispersion, qui se propagera dans la métapopulation jusqu'à ce que la mortalité naturelle ou par pêche l'épuise. La série chronologique de taux de dispersion révèle que sept fortes vagues de dispersion se sont produites depuis 1951. La dispersion est un processus important parce qu'il a tendance à stabiliser la distribution spatiale des reproducteurs dans la métapopulation et prolonge la longévité des populations locales moins productives de deux façons : 1) la réaction de dispersion dépendante à la densité accroît le taux de fidélité lorsque la population est à la baisse et (2) les populations à la baisse ont tendance à accueillir un plus grand nombre de migrateurs qu'elles n'en perdent par rapport aux autres populations. La dispersion est également importante parce que les vagabonds recolonisent des frayères nouvelles ou inoccupées. Cela permet à la métapopulation de s'adapter aux changements d'habitat et de modifier sa distribution spatiale en réponse aux tendances climatiques peu fréquentes et à d'autres facteurs.

INTRODUCTION

In the past decade there has been a renewed interest in studying the spatial structure of natural populations, because it is now widely recognized that most animals live and reproduce in fragmented habitats. In this context, McQuinn (1997) reviewed the ecological characteristics of Atlantic and Pacific herring and concluded that the stock structure of these species resembled a *metapopulation*. A metapopulation is simply a set of interacting, local breeding populations, which are linked by dispersal (gene flow). Dispersal is important because it can have a significant effect on the production dynamics and genetic differentiation of local populations. Metapopulation theory also recognizes that some populations can disappear for a time, because of a temporary loss in the amount (or quality) of the spawning habitat, recruitment failure, or simply by chance. However, when suitable conditions return these vacant habitats can be recolonized by migrants from nearby populations (Hanski and Simberloff 1997). Extensive research indicates that the spawning habitat of B.C. herring is indeed fragmented, and that herring disperse between these fragments both within and between stock assessment regions (Hay et al 1999). Ware et al (2000) reanalyzed a subset of the tagging data for the five, major migratory herring populations in B.C. (Fig. 1). They found that these populations were linked by dispersal; that the dispersal pattern matched an isolation by distance model; and that dispersal rates increased as the abundance of spawners approached the carrying capacity.

Ware and Schweigert (2001) analyzed the production and dispersal dynamics of the five major BC herring populations during the 1977-98 "warm" climate regime, and incorporated the results into a structured metapopulation model (SMP). Models of this form contain an explicit description of the local dynamics of the component populations, and include the effects of dispersal on population growth rates (Hanski 1996). The model was used to estimate the theoretical population carrying capacities of BC herring during the 1977-98 warm regime, and to explore the implications of dispersal on the dynamics of the local populations.

The purpose of this paper is to summarize existing information on the population dynamics and dispersal rates of the major BC herring stocks during the cool (1951-76), and subsequent warm (1977-98) climate regimes, and to assimilate these results into the metapopulation model. We use the model: 1) to quantify the amount of dispersal that probably occurred among the major herring populations during these periods, and 2) to assess the impact of dispersal on the dynamics of the populations and on the theoretical unfished carrying capacity of the metapopulation. We also evaluate the resilience of the five local populations to harvesting. For more background information about the basic biology of British Columbia herring stocks and the history of the fishery the reader is referred to an excellent review by Stocker (1993).

METHODS

Data Sources. Time series of spawner biomass, and age 2+ pre-recruit biomass for each population were obtained from the 2q version of the age-structured, stock assessment model (ASModel) where q after 1987 = 1 (see Schweigert 2001). Additional catch, age composition and weight-at-age data were obtained from the Pacific Biological Station herring database. The methods used to estimate the straying rates in this paper and the limitations of the data are discussed in detail in Ware et al (2000).

Metapopulation Structure. Five, major migratory herring stocks (Fig. 1) and a number of minor stocks are currently recognized in BC for management purposes (Schweigert 2001). This paper focuses on the dispersal rates and dynamics of the five major stocks. For convenience, we assume that the "population" boundaries are the same as the "stock" boundaries, so we use the two terms interchangebly. The metapopulation model developed by Ware and Schweigert (2001), estimates the prefishery biomass (PFB) of each population just before the roe fishery in the spring. In the model, a year begins in March/April of year *t* and ends in March/April of the following year (*t+1)*. The model keeps track of the biomass leaving and entering the age 2+ (and older component) of each population due to: recruitment, fishing, spawning, dispersal (immigration and emigration), growth, and natural mortality. The five local populations are linked in the model by an empirically based distance- and density-dependent dispersal process (discussed below). Dispersal is presumed to occur after spawning when the adult fish are on the offshore feeding grounds. An isolation by distance relationship is used to describe where the migrants go (i.e. the dispersal pattern). Fish, which migrate and are imported to other populations are presumed to grow and die at the same rates as the fish in the destination population. The SMP model also contains a partial recruitment scheme. The biomass of age 2+, 3+ and 4+ recruits that join the inshore prefishery biomass in year *t* is determined by population and age-specific availability factors calculated by the age-structured model (Schweigert 2001).

The structure of the metapopulation model is illustrated in Fig. 2. The model contains the following variables and notation: j = local source population, k = destination population, t = year.

- *Prefishery biomass* ($PFB_{j,t}$, kt). Biomass of the fully-recruited adult component (ages 2+ and older) of population *j* on the spawning grounds just before the roe fishery occurs in year *t*.
- *Catch*$_{j,t}$ (kt), the amount of biomass removed from population *j* by the fishery in year *t*.
- *Harvest rate*$_{j,t}$ (HR), defined as $Catch_{j,t}/PFB_{j,t}$.
- *Spawner biomass* ($SB_{j,t}$, kt). Biomass of fish in population *j*, which survive the fishery and spawn ($SB_{j,t} = PFB_{j,t} - Catch_{j,t}$).
- *Spawn*$_{j,t}$ deposited by population *j* in year *t*, calculated as $0.23*SB_{j,t}$. The proportionality constant assumes a 50:50 sex ratio (see Ware and Tanasichuk 1989).
- *Adult biomass in population j after spawning* and before dispersal occurs ($IB_{j,t}$, kt). $IB_{j,t} = SB_{j,t} - Spawn_{j,t}$.
- *Dispersal rate* ($DR_{j,t}$). Proportion of herring in population *j* that disperse to other populations according to some user defined function (see below).
- *EXPORT*$_{j,t}$ *(Emigration)*. Biomass (kt) of herring that disperse from population *j*. $Export_{j,t} = DR_{j,t}*IB_{j,t}$.
- *IMPORT*$_{j,t}$ *(Immigration)*. Biomass (kt) of herring that disperse to population *j* from the other four populations in year *t*.
- *Population specific instantaneous natural mortality rate* (M_j, yr^{-1})
- *Population specific survival rate*, defined as $\exp(-M_j)$.
- *Population specific adult growth rate* defined as $\exp(G_j)$, where G_j is the instantaneous growth rate.

- *Remaining biomass* (*$RB_{j,t}$*, kt*)*. Biomass of adult herring in population *j* that did not disperse. $RB_{j,t} = IB_{j,t} – Export_{j,t}$.
- *Pre-recruits* (*$PRB_{j,t}$*, kt*)*. Biomass of all age 2+ herring (kt) in population *j* on the offshore feeding banks in year *t*.
- *$Recruits_{j,t}$* . Biomass (kt) of pre-recruit herring that migrate inshore and enter the prefishery biomass of population *j* on the spawning grounds in year *t*. The proportion of the pre-recruit biomass that joins the $PFB_{j,t}$ is determined by population and age-specific *availability $factors_j$* calculated by the age-structured model (see Schweigert 2001). Recruitment of age 2+ fish occurs with a 3-yr time delay in the model according to some user defined stock-recruitment function (see below), or by a recruitment time series estimated by the age-structured model.
- *Repeat Spawners* (*$RS_{j,t\ initial}$*, kt*)*. The initial size of the repeat spawner pool in population *j* at the beginning of the growing season in year *t*: $RS_{j,t\ initial} = RB_{j,t} + R\_Recruits_{j,t}$.
- *$R\_Recruits_{j,t}$* . This is the biomass of age 2+ to age 4+ pre-recruits, which did not spawn in year *t* but will spawn in *year t+1*. These fish join the repeat spawner pool in population *j* on the offshore feeding banks after the spawning season in year *t* according to their population and age specific availability factors.

RESULTS

Northeast Pacific Climate Regimes. The herring time series spans two major climate regimes in the Northeast Pacific Ocean: the 1945-76 “cool” regime and the 1977-98 “warm” regime (Fig. 3). During the 1945-76 cool regime the annual average temperature was below the long-term mean, but was punctuated by five scattered years with positive temperature anomalies. The largest positive anomalies were associated with the 1958 and 1963 el Ninos. After the well-documented climate regime change in 1976, average water temperatures were consistently above the long-term mean until 1999, except for two years. The next anticipated climate regime change may have occurred in 1999 (Ware 1995). Since then average water temperatures have been below the long-term mean. We find it convenient to refer to the 1945-76 period as a “cool” climate regime and to the 1977–98 period as a “warm” climate regime. However, in doing so we realize that we are greatly oversimplifying the contrasts in ocean conditions that occurred between these two periods, and that some of the differences in herring dispersal and productivity rates that we found are almost certainly related to collateral changes in other climatic and ecosystem-based factors besides ocean temperature.

Fishery. A herring meal and reduction fishery began in BC in 1935 (Hourston 1980). By 1940 all of the coast was being heavily fished. The total catch increased from about 25 kt in 1935 to about 240 kt in 1963. When a series of poor year classes recruited in the mid-1960s, catches remained high. Consequently, the fishery removed most of the mature adults and large numbers of age 2 and age 1 fish before depletion became evident, and the reduction fishery was closed in 1968 (Stocker 1993). The fishery remained closed for the next four years to allow the stocks to rebuild. In response to a high demand from Japan, a commercial roe herring fishery began in 1972 and has been the dominant component of the fishery since then. This change in the nature of the fishery resulted in the stocks being harvested at very different rates during the two climate periods (Table 1).

Table 1. Average catches (kt) and harvest rates during 1951-76 (Period 1) and 1977-98 (Period 2). Data source: Schweigert (2001).

Stock	Average catch Period 1 (kt)	Average harvest rate	Average catch Period 2 (kt)	Average harvest rate
WCVI	18.0	0.38	8.2	0.21
Georgia Strait	35.2	0.59	12.8	0.19
Central Coast	18.2	0.62	7.1	0.24
QCI	10.1	0.40	4.0	0.16
PRD	18.1	0.47	5.2	0.18
Total	99.6	0.50	37.3	0.20

Spawner Biomass. The average total prefishery biomass of the stocks between 1951-76 was only slightly higher than it was between 1977-98 (Table 2). However, because harvest rates were higher during the reduction fishery era the average spawner biomass was much lower between 1951-76 than it was between 1977-98, particularly in the Georgia Strait, Central Coast and Queen Charlotte Islands stocks (Table 2).

Table 2. Average prefishery (PFB) and spawner biomass (SB) during 1951-76 (Period 1) and 1977-98 (Period 2). Data source: Schweigert (2001).

Stock	Average PFB Period 1 (kt)	Average SB Period 1(kt)	Average PFB Period 2 (kt)	Average SB Period 2 (kt)
WCVI	47.8	29.7	38.8	30.6
Georgia Strait	59.6	24.4	65.5	52.7
Central Coast	29.5	11.3	30.0	22.9
QCI	25.4	15.3	25.7	21.7
PRD	38.3	20.2	28.7	23.5
Total	200.6	100.9	188.7	151.4

Density-Dependent Dispersal. Ware and Schweigert (2001) found that the dispersal rate ($DR_{j,t}$) of mature herring from population *j* in year *t* was positively correlated with the biomass of spawners in the population ($SB_{j,t}$) in the same year. A logistic model fit the warm period tagging data (collected between 1982-1991) better ($R^2 = 0.85$) than a linear model ($R^2 = 0.79$):

$$DR_{j,t} = 0.33 / [1+ 7.1EXP(-0.081SB_{j,t})]$$

Tagging data collected during the early 1950s were also analyzed to determine if the dispersal rate was density-dependent (Tables 2 and 3). The results indicate that the dispersal rate was positively correlated with the spawner biomass in the Georgia Strait and Central Coast populations. However, in the Prince Rupert District population there was no correlation *over the observed range in spawner biomass*. Unfortunately, there were either insufficient data (in QCI), or insufficient contrast in spawner biomass (in WCVI) to evaluate if there was a relationship in these populations. So the results for the cool base period are suggestive, but equivocal: *in two of the three cases with a reasonable contrast in SB, the dispersal rates appeared to be density-dependent.*

Table 3A. Interannual variability in the dispersal rates from each population, in years where 12 or more tags were recovered. The dispersal rate was calculated as (1- x/y), where x is the number of tags that were released (in year t) and recovered (in year t+1) in the indicated stock area (j), and y is the total number of tags released (in year t) from stock (j) that were recovered from all stock areas (in year t+1). Hence the dispersal rate = (1- fidelity rate). There were no releases or recoveries in SA19, 28 and 29 or in Section 132, so dispersal rate estimates for the Georgia Strait stock do not include herring from these areas. Data source: Ware et al 2000.

Release Year t	WCVI (SA 23,24,25)	Georgia Strait (SA 14-18)	Central Coast (SA 6,7,8,9)	QCI (SA 0,2)	PRD (SA 3,4,5)
1950	0.112	0.167	0.098	.	0.042
1951	0.008	0.028	0.144	.	0.058
1953	0.026	0.261	0.040	.	0.017
1954	.	0.024	0.111	0.052	0.032
1981	.	.	.	.	.
1982	0.150	.	.	.	.
1988	.	.	.	.	.
1989	0.313	0.333	0.194	.	.
1990	0.261	0.333	0.184	(0.356*)	.
1991	.	.	.	0.143	.

* This value is an outlier and was excluded from the analysis (see Ware et al 2000).

Table 3B. Estimated spawner biomass (kt) in each population during the tag release years (t) (from Schweigert 2001). Spawner biomass in 1950 was estimated by multiplying the recorded length of spawn (km) by the average spawner density (tonnes/km) in each population.

Release Year t	WCVI (SA 23,24,25)	Georgia Strait (SA 14-18)	Central Coast (SA 6,7,8,9)	QCI (SA 0,2)	PRD (SA 3,4,5)
1950	20.0	18.3	16.7	.	30.5
1951	19.1	22.6	16.3	.	23.2
1953	18.4	53.9	11.0	.	30.2
1954	.	34.4	10.3	19.6	9.7
1981	.	.	.		.
1982	27.1	.	.	.	.
1988	.	.	.	.	.
1989	47.0	47.8	32.4	.	.
1990	40.1	67.9	29.8	22.5	.
1991	.	.	.	12.9	.

We estimated a common dispersal rate relationship for both climate regimes by combining the data in Tables 3A and 3B (Fig. 4). A logistic model fit the aggregated data better (adjusted-r^2 = 0.58) than a linear model (adjusted-r^2 = 0. 53) and produced a slightly smaller RMS error; so we used the logistic model:

$$DR_{j,t} = 0.33/ [1+ 17.7EXP(-0.082\ SB_{j,t})] \qquad \textbf{1.}$$

An additional test was performed to determine how well eq.1 fit the cool regime data. We found that when the 1950s data were fit to a separate logistic function the cumulative RMS error for that period was 0.82. By comparison, the cumulative RMS error for the 1950s estimated by applying eq. 1 was only slightly larger (0.94). We therefore choose the simplest explanation and conclude that eq. 1 describes how the dispersal rate changes with spawner biomass during both climate regimes. However, we note that the slight offset in the fit of the 1980s data to eq. 1 (Fig. 4) suggests that the dispersal rates might be slightly higher for a given biomass during "warm" regimes. The possibility that there is an additional "regime-effect" should be examined when new tagging data become available.

Distance-Dependent Dispersal Pattern. There is a significant correlation between the proportion of herring that disperse to other populations and the degree of separation between where the fish were tagged, and where they were recovered one year later (Ware et al 2000). The resulting relationship can be adequately described by a negative exponential equation:

$$Y = A\ \mathrm{EXP}(-B\ X), \qquad \mathbf{2a.}$$

where Y = proportion of fish dispersing distance X (km) in one year. Because the tag release and recovery locations were known with far more precision during the 1980s than they were in the 1950s, the variability in the 1950s was much larger than it was in the 1980s (Ware et al 2000).

The simplest hypothesis is that *a common isolation by distance relationship applies to both periods*. To test this we estimated the parameters in eq. 2a for each period:

Period	A (95% CL)	B	R^2
1980s	0.75 (0.32-1.18)	0.0028	0.49
1950s	0.93 (-0.26-2.12)	0.0032	0.22

The exponential rate constants (B) in both periods were similar. However, the uncertainty in the 1950s intercept (A) was much larger. Because the latter falls within the 95% confidence interval of the 1980s intercept, we conclude that there is insufficient evidence at this time to falsify the hypothesis that a common isolation by distance relationship applies in both periods. Accordingly, we assume that the proportion ($P_{j,k}$) of herring dispersing from population *j* to population *k* in year *t* is given by the following equation:

$$P_{j,k} = 0.75 \exp(-0.003\ D_{j,k}) \qquad \mathbf{2b.}$$

where $D_{j,k}$, (km) is the distance between the source (*j*) and destination (*k*) populations (Fig.5).

Using the distances in Table 4, equation 2b was used to calculate the dispersal pattern (P_{jk}) shown in Table 5.

Table 4. Distances ($D_{j,k}$, km) between the the geographical centers of each population. These are the shortest distances that fish could migrate between populations.

	WCVI_k	GS_k	CC_k	QCI_k	PRD_k
WCVI_j	● .	274	447	596	713
GS_j	274	●	434	622	776
CC_j	447	434	●	202	303
QCI_j	596	622	202	●	197
PRD_j	713	776	303	197	●

Table 5. The dispersal pattern from source population *j* to destination population *k*. The relative proportions calculated from eq. 2b were normalized so the proportion of herring exported from each population to the other four populations was equal to 1. This normalization procedure causes the dispersal pattern matrix to become slightly asymmetrical, because the *average* distance between the source population and the other four populations is different for each source population (see Table 4). For example, the average distance between the QCI population and the other populations is 346 km, while the average distance between the Georgia Strait population and the other populations is much larger (524 km). These differences create an asymmetry in the dispersal matrix .

	WCVI$_k$	GS$_k$	CC$_k$	QCI$_k$	PRD$_k$
WCVI$_j$	**.**	0.446	0.265	0.169	0.119
GS$_j$	0.456	**.**	0.282	0.160	0.101
CC$_j$	0.176	0.184	**.**	0.368	0.272
QCI$_j$	0.117	0.109	0.384	**.**	0.390
PRD$_j$	0.100	0.083	0.344	0.473	**.**

Dispersal. Output data from the age-structured model (Tables 1 and 2), the density-dependent straying rate (eq. 1) and the isolation by distance dispersal pattern (Table 5) were used to estimate the average dispersal rates from each population during the reduction and roe fishery periods (Tables 6 and 7).

Table 6. Estimated average annual dispersal of age 2+ (and older) biomass (kt/yr) from source population *j* to destination population *k* during the reduction period. The row totals indicate the total biomass exported from the source population in that row, while the column totals indicate the total biomass imported to the destination population in that column.

Population	WCVI$_k$	GS$_k$	CC$_k$	QCI$_k$	PRD$_k$	Total Export
WCVI$_j$	.	1.331	0.791	0.504	0.355	2.981
GS$_j$	0.831	.	0.514	0.291	0.184	1.820
CC$_j$	0.063	0.066	.	0.131	0.097	0.357
QCI$_j$	0.076	0.071	0.249	.	0.253	0.649
PRD$_j$	0.117	0.097	0.402	0.553	.	1.169
Total Import	1.087	1.565	1.956	1.479	0.889	**6.976**

Table 7. Average dispersal of age 2+ (and older) biomass (kt/yr) from source population *j* to destination population *k* during the roe fishery period. The row totals indicate the total biomass exported from the source population in that row. While the column totals indicate the total biomass imported to the destination population in that column.

Population	WCVI$_k$	GS$_k$	CC$_k$	QCI$_k$	PRD$_k$	Total Export
WCVI$_j$	.	2.06	1.31	0.96	0.57	4.90
GS$_j$	5.55	.	3.73	1.81	1.11	12.20
CC$_j$	0.55	0.46	.	1.01	0.79	2.81
QCI$_j$	0.25	0.28	1.02	.	0.92	2.47
PRD$_j$	0.29	0.26	0.97	1.43	.	2.95
Total Import	6.59	3.06	7.03	5.21	3.36	**25.33**

Adult Growth and Mortality Rates. Population-specific instantaneous growth rates ($G_{j,t}$) were estimated for each year in the time series (1951-98). First, we calculated the age-specific instantaneous growth rates. These age-specific estimates spanned the period *immediately after spawning* in year *t*, to *immediately before spawning* in year *t+1*. Accordingly, our growth estimates account for the considerable loss of body mass associated with spawning. This is important because spawning in herring depletes the mature stock biomass by about 23%. Finally, we calculated the average population-specific instantaneous growth rates (G_j), by weighting the average age-specific instantaneous growth rates in year *t* by the available proportion of mature fish at each age in the population in the same year, and averaging the results for each climate regime (Table 8).

Table.8. Population-specific average adult growth rates (G_j) during the cool and warm periods, and the probability that the rates during these two periods are significantly different.

Population	Cool G_j (yr^{-1})	Warm G_j (yr^{-1})	Probability
WCVI	0.438	0.479	0.61
GS	0.447	0.460	0.11
CC	0.423	0.379	0.13
QCI	0.447	0.344	0.002
PRD	0.425	0.355	0.006
Average	0.436	0.403	

Table 8 shows that the average growth rates during the cool regime were slightly lower in the two southern populations (WCVI and GS), but higher in the three northern populations. A t-test indicated that the growth rates during the cool regime were significantly higher ($P<0.05$) in the QCI and PRD populations, but not in the Central Coast population.

The population-specific natural mortality rate estimated by the age-structured model (ASM-M_j) is really a *net loss rate*, which includes real natural mortality plus the "hidden" effects of immigration and emigration (Ware and Schweigert 2001). Therefore, we calculated a time-averaged, adjusted-M (M_j) to account for dispersal between the populations (see appendix 1). The results are summarized in Table 9.

Table.9. Population-specific natural mortality rates (M_j) adjusted for dispersal during the cool and warm climate periods, and the age-structured model estimate of the net loss rates (ASM-M_j).

Population	ASM-M_j	Cool M_j (yr^{-1})	Warm M_j (yr^{-1})
WCVI	0.444	0.376	0.501
GS	0.539	0.246	0.332
CC	0.278	0.180	0.453
QCI	0.500	0.517	0.608
PRD	0.379	0.163	0.424
Average	0.428	0.296	0.464

A t-test using the five population means for each period as independent estimates suggests that there is a 92% chance that the warm period natural mortality rate was higher than the cool period rate.

Spawner-Recruit Relationships. The underlying relationship between spawner biomass and recruit biomass is a fundamental issue in population dynamics because it describes how a key component of population production varies with stock size. Contrary to some prevailing views, ecological theory is very clear on the point that there is some underlying biological relationship between spawners and recruits. However, what is unclear and is therefore debated is: What is the functional form of this relationship? Instead of approaching the raw data with a preconceived notion of what the underlying relationship was, we plotted the pre-recruit biomass in year *t+3* against the parent spawner biomass in year *t* . The resulting scatterplots were then smoothed using a distance weighted least squares regression (DWLS, Systat). This regression procedure fits a line through a set of points by least squares. However, unlike linear or low order polynomial smoothing, the surface is allowed to flex locally to fit the data better. This method produces a true, locally weighted curve, where data points far from a selected point contribute little to the prediction and data points near contribute the most (Wilkinson et al 1996). The DWLS analysis indicated that the underlying relationship between recruitment (PRB_j) and parent stock biomass (SB_j) resembled either a dome-shaped curve, or a "hockey stick" relationship.

Accordingly, we evaluated three models to determine which one provided the best fit to the spawner-recruit data for each population, and period:

Hockey stick: If (SB<TSB) Then (k*SB) Else (PRB_{max})

Ricker: PRB = a*SBExp(-b*SB)

Ware: PRB = 1/((c*Exp(d*SB)/SB) + f)

In the hockey stick model, recruitment increases linearly with SB_j until the latter reaches a threshold biomass (TSB_j). *Above the TSB, recruitment maintains an average saturating value of* PRB_{max}. Barrowman and Myers (2000) examined the properties of the hockey stick model and found that it usually gave a lower estimate of the slope at the origin than the Beverton-Holt model. Consequently, the Beverton-Holt model tends to overestimate the resilience of a population to fishing and its carrying capacity compared to the hockey stick model. For these reasons, we considered the latter model to be more appropriate for our purposes than the Beverton-Holt relationship, even though both models might fit a noisy set of data equally well. For the dome-shaped relationships we tested the 2-parameter Ricker model and the 3-parameter Ware (1980) model. In the Ricker model, recruitment initially rises with respect to SB to some maximum average value (PRB_{max}), and then declines at higher levels of SB. The 3-parameter Ware model, describes a family of curves which range in shape from a saturating Beverton and Holt-like relationship to a complex dome-shaped curve. Because it has an additional parameter, the Ware model is able to "find" a more complex shaped curve in the raw data than the Ricker model.

The results of the spawner-recruit analysis are summarized below for each population. The supporting details are provided in Appendix 2.

WCVI Recruitment. *Year-classes born during the cool period in this population were 1.8 x larger (mean pre-recruit biomass (PRB) = 25.4 kt) than they were during the 1977-98 warm period (mean PRB = 13.8 kt). This difference is highly significant (p=0.006).* DWLS analysis indicated that during the cool period recruitment declined when the spawner biomass was at the high end of its range. This decline was confirmed by the Ricker and Ware models, which provided the best fit to the data. The Ricker and Ware models suggest that maximum recruitment (averaging 31-33 kt) occurs when the spawner biomass is about 36 kt (Fig. 6; Appendix 2). In contrast, during the warm period, recruit biomass was independent of the spawner biomass over the range of available data. So the data were fit to a hockey stick model (Ware and Schweigert 2001).

Georgia Strait Recruitment. Year-classes born during the cool period in this population were 1.15 x larger (mean pre-recruit biomass (PRB) = 32.7 kt) than they were during the warm period (mean PRB = 28.4 kt). However, because of the large interannual variability the difference is not statistically significant (p=0.42). DWLS analysis indicated that during the cool period recruitment declined at high spawner biomasses. This decline was confirmed by the Ware model, which provided the best fit to the data (Fig. 6; Appendix 2). In this case, a recruitment maxima (averaging 50 kt) occurred when the spawner biomass was about 28 kt. In contrast, during the warm period there was no evidence of a decline in recruitment at high spawner biomasses. So the data were fit to a hockey stick model.

Central Coast Recruitment. Year-classes born during the cool period in this population were 1.17 x larger (mean pre-recruit biomass (PRB) = 13.4 kt) than they were during the warm period (mean PRB = 11.4 kt). Again because of the large interannual variability in each period this difference is not statistically significant (p=0.57). DWLS analysis indicated a slight decline in the pre-recruit biomass when the spawner biomass was at the high end of its range. This decline was confirmed by the Ware and Ricker models, which provided slightly better fits to the data (Appendix 2; Fig.6). In contrast, during the warm period there was no evidence of a decline in recruitment at high spawner biomasses. So the data were fit to a hockey stick model.

Queen Charlotte Islands Recruitment. *Year-classes born during the cool period in this population were 1.8 x larger (mean pre-recruit biomass (PRB) = 14.3 kt) than they were during the warm period (mean PRB = 7.9 kt). This difference is significant (p=0.037).* DWLS analysis indicated that during the cool period recruitment declined at high spawner biomasses. This was confirmed by the Ricker and Ware models which provided better fits to the data (Fig. 6; Appendix 2). In contrast, during the warm period there was no evidence of a decline in recruitment at high spawner biomasses. So the data were fit to a hockey stick model.

Prince Rupert District Recruitment. Year-classes born during the cool period in this population were 1.12 x larger (mean pre-recruit biomass (PRB) = 14.0 kt) than they were during the warm period (mean PRB = 12.6 kt). This difference is not statistically significant (p=0.67). During the cool period, the DWLS analysis indicated no apparent decline in the pre-recruit biomass when the spawner biomass was at the high end of its range. So the data were fit to a hockey stick model (Fig. 6; Appendix 2). In contrast, during the warm period a Ricker model provided the best fit to the data. This finding makes the PRD population standout as a curious anomaly: during the cool period the spawner-recruit relationship in this population was dome-shaped, whereas in the other four populations it wasn't. Similarly, during the warm period the PRD spawner-recruit data fit a hockey stick model, whereas in the other four populations the relationship was dome-shaped. So for some unknown reason, the spawner-recruit dynamics of the PRD population appears to be different from the other four populations.

Carrying Capacity (SBj^{*}). The theoretical unfished carrying capacity of a population is determined by all the rate processes that add and remove biomass from the population. At equilibrium, the new biomass contributed by recruitment, growth and dispersal (import) equals the losses removed by spawning, export, and natural mortality. The theoretical carrying capacity of spawners (SB_j^{*}) was estimated for each population and period by: 1) setting the harvest rate to zero; 2) applying the best fitting population-specific stock-recruit relationships for each period (the shaded relationships in Appendix 2 Table), and 3) applying the dispersal-adjusted natural mortality rates for each period (Table 9); the common dispersal rate function (eq. 1); and the common isolation by distance dispersal pattern (Table 5).

The results suggest that the carrying capacity of the metapopulation was more than twice as large during the cool regime (Table 10) There was also a striking reversal in the size of the local populations. During cool regimes, the PRD and Central Coast populations appear to have the largest carrying capacities (however, we note that these carrying capacities may be overestimated, because the estimated natural mortality rates for these populations were anomalously low (Table 9). If the true mortality rates were higher then the carrying capacities would be smaller). In contrast, during protracted warm regimes, Georgia Strait has the largest carrying capacity. The other four populations were considerably smaller.

Table 10. Theoretical carrying capacity of spawners (SB^{*}) in each climate regime and the adult herring biomass exported by each population at (SB^{*}).

Population	Cool SB^{*} (kt)	Cool Export (kt/yr)	Warm SB^{*} (kt)	Warm Export (kt/yr)
WCVI	107	27	57	13
Georgia Strait	97	25	93	23
Central Coast	135	34	49	10
QCI	79	20	32	4
PRD	166	42	37	5
Total	**584**	**148**	**268**	**54**

Resilience to Havesting The resilience of the local populations to harvesting during a protracted warm regime was explored by "fishing" the metapopulation at different target rates. During each simulation the local populations were fished at the same rate and dispersal was assumed to occur. The results suggest that the populations have the following inherent resilience to fishing (in order from lowest to highest): QCI<CC<WCVI<PRD<GS (Fig. 7). This implies that the QCI population is likely to be near its Cutoff biomass more frequently than the other populations, while the GS and PRD populations are unlikely to approach their Cutoffs with the current 20% target harvest rate. The Cutoff is a commercial roe fishery reference point. If the forecast biomass of a population is below its Cutoff then the roe fishery is closed (see Schweigert 2001).

Time-Varying Net Dispersal Rates A variation of the metapopulation model (SMP-D) was developed to estimate the annual amount of dispersal between 1951-1998. In this case we input the respective annual catch time series, the ASModel recruit biomass time series, and the growth rate time series for each population. The *net dispersal rate* was then estimated by subtracting the simulated biomass exported from population *j* in year *t* from the biomass imported to population *j* in year *t*. The resulting net dispersal time series output by the SMP-D model are shown in Figure 8, and summarized in Table 11.

Table 11. Average adult herring biomass exported and imported annually to each population between 1951-98 estimated by the SMP-D model. The net dispersal rate (import-export) and its coefficient of variation are also indicated. The slight difference in the total export and import in the metapopulation is caused by rounding errors.

Population	Average export (kt/yr)	Average import (kt/yr)	Average net dispersal (kt/yr)	Net dispersal CV
WCVI	4.86	4.92	0.06	72.1
Georgia Strait	7.62	3.12	-4.50	-1.2
Central Coast	3.70	6.12	2.42	0.9
QCI	3.03	5.50	2.47	1.3
PRD	4.43	3.53	-0.90	-3.6
Total	23.64	23.19		

Although these statistics summarize the average state, it would be misleading to characterize the populations as either *"net exporters" (sources)* or *"net importers" (sinks)* , because most populations switch from being net exporters to net importers or vice-versa in response to changing conditions within the metapopulation. For example, Figure 8 shows that the WCVI population was a net importer of biomass over most of the time series. However, it became a significant exporter during the 1970s when the biomass of this population was exceptionally large. Because of the large exports that probably occurred at that time, the WCVI population probably imported only slightly more biomass than it exported over the length of the time series (Table 11). In contrast, the Georgia Strait population has been a major exporter, except during a brief period in the late-1950s to early-1970s when the abundance of this population was low. Similarly, the Prince Rupert District population was also a major exporter, particularly during the mid-1950s to mid-1960s, and during the mid-1970s, and the mid-1980s. However, by the 1990s the PRD population may have been importing slightly more biomass than it exported (Fig. 8). The Central Coast population appears to have been a net importer over most of the time series. As has the QCI population, except for a brief period in the early 1980s when this population was dominated by the large 1977 year-class. The coefficient of variation suggests that the net disperal rate is most variable in the WCVI population. It is of interest to note that an analyses of the inter-annual variation in spawner biomass determined from a comparison of the spawn deposition in each stock assessment area and that expected from the deposition observed the preceding year (assuming average growth and survival rates) provide an independent estimate of the dispersal rates among stocks (Schweigert and Ware, unpubl. data). The results suggest dispersal patterns broadly similar to those determined from the population model, and provide confirmation of the apparent movement of spawners between adjacent assessment regions between years.

Correlation analysis of the net dispersal rate time series revealed a significant negative relationship between several adjacent populations (Table 12). In this case, a negative correlation implies that a large biomass exported (imported) from one of the correlated populations is significant enough to appear as a large import (export) in the other population. For example, variations in biomass exported from the Georgia Strait population tend to appear as variations in imports in the WCVI and CC populations, and vice-versa. It is important to recognize these correlated populations, because they appear to significantly influence each other's abundance.

Table 12. Correlations in the net dispersal rates between populations during the roe fishery period (after 1971; n=27).

Stock	WCVI	GS	CC	QCI	PRD
WCVI	•				
GS	**-0.74**	•			
CC	**-0.60**	0.24	•		
QCI	0.00	-0.39	-0.11	•	
PRD	-0.15	-0.03	0.14	**-0.55**	•

Dispersal Waves. Ware and Schweigert (2001) showed that when very large year-classes mature and recruit to one of the local populations they can set up dispersal waves, which ripple through the metapopulation until the size of the year-class (or year-classes) that caused them are depleted by natural and fishing mortality. Close inspection of Fig. 8 suggests that between 1951 to 1998 seven large dispersal waves probably occurred (Table 13).

Table 13. Timing and origin of the largest dispersal waves in the metapopulation and the populations that were most affected. The biomass of the most affected populations increased significantly in each case (see Fig. 8).

Period	Source population	Most affected populations
Early 1950s	Georgia Strait	WCVI, Central Coast
Late 1950s	WCVI	Georgia Strait
Late 1950s	PRD	QCI, Central Coast
Early 1970s	WCVI	Georgia Strait, Central Coast
Mid 1970s	PRD	QCI, Central Coast
Late 1970s	Georgia Strait	WCVI, Central Coast
Early 1980s	QCI	PRD, Central Coast

DISCUSSION

Many herring stakeholders and environmental groups still believe that the five, major migratory BC herring stocks are "discrete" populations. This perspective is not supported by the ecological and genetic evidence. The tagging data (Hay et al 1999; Ware et al 2000) and the resulting dispersal rate estimates in this paper clearly indicate that there is extensive movement of individuals (and genes) between populations; and that this rate of exchange is large enough to ensure that there is unlikely to be any genetic differentiation between the five major stocks. This hypothesis was recently confirmed by an independent DNA analysis (Beacham et al 2001). Although the ecological and DNA information are consistent on the point that there should be very little genetic differentiation between the major stocks, several minor herring stocks that are more geographically, or reproductively isolated may be more differentiated.

A comparison of population statistics between the 1951-76 cool climate regime and the 1977-98 warm regime reveals some significant differences. Harvest rates were much higher (mean=0.49) during the reduction fishery, which dominated most of the cool regime, than they were during the roe fishery period, which prevailed during the warm regime (mean=0.20). Consequently, the total biomass of spawners in the metapopulation was much lower during the cool regime (mean = 101 kt) than it was during the warm regime (mean=151 kt). During the cool regime, this smaller biomass of spawners resulted in a generally lower dispersal of fish through the metapopulation. There were also some striking differences in the production characteristics of the local populations between regimes. During the 1951-76 cool regime, population growth rates (G) were lower in the two southern populations, but were higher in the three northern populations. In contrast, the dispersal-adjusted natural mortality rates (M_j) were lower everywhere during the cool regime (mean = 0.30), compared to the warm regime (mean=0.46); there is a 92% probability that this difference is significant. With respect to recruitment, the mean pre-recruit biomass was higher in all populations, and was significantly higher in the WCVI and QCI populations during the 1951-76 cool regime. Perhaps our most curious finding was the reversal in the shape of the spawner-recruit relationship between cool and warm regimes. During the warm regime, the underlying form of the stock-recruit relationship resembled a hockey stick function everywhere except in the PRD stock where the relationship was clearly dome-shaped (Ware and Schweigert 2001). In contrast, during the cool regime there was a complete reversal of this pattern: the spawner-recruit relationship was dome-shaped everwhere except in the PRD stock, where the relationship resembled a hockey stick. Although we don't understand why these differences and reversals occurred, they emphasize that the underlying form of the recruitment pattern is not the same in every local population, and that the shape of the relationship may change in reponse to shifts in climate. This is important because the form of the spawner-recruit relationship has a large effect on the dynamics of the five major populations, which are the current units for managing the fishery.

The metapopulation model outlined above incorporates the extent of our knowledge about dispersal in B.C. herring. The model contains two important functional relationships: a density-dependent dispersal rate, and an isolation by distance dispersal pattern. Density-dependent dispersal has been observed in other animal populations (Burgman et al 1996). However, we are not aware of any other herring studies, which have reported increases in dispersal rates with population size. Probably because the expensive, multi-year tagging programs required to obtain such data have not been conducted. Olivieri and Gouyon (1997) considered why dispersal may have evolved. Overall, they noted that there exists a selection for residency within each local population. However, there are factors like avoidance of sibling competition and more favorable conditions elsewhere that will select for migration. Dispersal should be favored when there is significant variability in the size of nearby populations, which there is in BC herring. The global persistence of any genotype requires colonization after local extinction. Olivieri and Gouyon argue that, given enough time, all local populations will eventually go extinct, so only genotypes that have migrated will be able to reproduce and persist. Hence, while there may be short-term disadvantages to migration, there may be significant long-term benefits.

Expanding on these arguments, we believe there is also a selective advantage for the dispersal rate to increase when the spawning and juvenile rearing habitat becomes more crowded. Pacific herring populations in BC have high natural mortality rates (M averages about 0.46 yr^{-1}), so their expected reproductive lifespan is only a few years. When the biomass of a population increases and approaches its carrying capacity, the underlying spawner-recruit relationship causes a sharp decline in the biomass of recruits produced by each spawner (R/S). Consequently, as the number of spawners increases in a population it may be advantageous for a higher proportion of individuals to disperse after spawning. Simply by chance, some of these migrants will join nearby populations that are smaller (relative to their carrying capacity), so the migrants may end up producing more recruits over their short reproductive lifespans then the individuals that stayed in the source population. Conversely, there will be a strong selection for residency in a declining population because, all else being equal, each spawner should be able to produce more recruits (higher R/S), due to an improvement in the quality of the spawning and juvenile rearing habitats. A principal objective of the new coded wire tagging program for herring, which began in 1999 (Schweigert and Flostrand 2000) should be to determine if the dispersal rate of B.C. herring is density-dependent as the existing (but limited) data suggest; and if the dispersal rate function is population-specific, or if it can be described by a common relationship as we were forced to assume.

Studies of natural populations have found that dispersal tends to be higher between populations that are geographically close, and that the decline in the dispersal rate with distance can often be described by a negative exponential function (Burgman et al 1996). After analyzing B.C. herring tagging data collected between 1936 to 1951, Taylor (1964) observed that mixing was "greatest between adjacent populations and became less between those farther apart". Ware et al (2000) found the same relationship in tag release and recovery data collected three decades later during the 1980s. Consequently, an isolation by distance dispersal pattern appears to be a persistent ecological characteristic of B.C. herring. Dispersal between the WCVI and Georgia Strait populations probably occurs on the feeding grounds on the continental shelf off southwest Vancouver Island. Similarly, the Central Coast, Georgia Strait, WCVI, and QCI populations probably exchange individuals around the Goose Island Bank in Queen Charlotte Sound in the summer. While PRD, CC and QCI herring may be partially mixing in summer feeding areas in Hecate Strait. Another high-priority objective of the coded wire tagging program should be to determine if the isolation by distance straying pattern shown in Fig. 5 is relatively robust, or if it is modified by variations in environmental conditions.

One weakness of our model is that it only accounts for the dispersal of adults. Some very limited data suggest that juvenile herring (i.e. ages 0+,1+ and 2+) have a higher tendency to disperse (Hourston 1959). We didn't include this component in the metapopulation model because other than Hourston's observation, nothing is known about the dispersal of juveniles. This is one aspect of herring ecology that requires more research. It is important, because a significant number of fish that eventually recruit to a population may have migrated there from nearby populations.

During the last 50-yrs the estimated net dispersal rates imply that the Georgia Strait and PRD populations have tended to be major exporters of adult herring to nearby populations, while the

Central Coast and QCI have been major importers (Fig. 8). We found a highly significant positive correlation between the net dispersal time series and the stock assessment spawner biomass difference time series in the WCVI and PRD populations (Fig. 9; Appendix 3). This suggests that a large part of the observed difference in spawner biomass estimated by the escapement and ASModels in these populations may be caused by dispersal. From a stock forecasting perspective, dispersal probably has the largest effect on the accuracy of the forecasts when an exceptionally large year-class (or classes) recruit to one of the local populations. When this occurs a significant proportion of the resulting adult biomass is exported to nearby populations. This sets up a dispersal wave which decreases in height as it moves further away from the source population. These dispersal waves radiate around the metapopulation until they are depleted by natural and fishing mortality (Ware and Schweigert 2001). The dispersal time series suggest that seven large dispersal waves probably occurred between 1951-1998.

During a protracted warm regime, the QCI population appears to be less resilient to fishing than the Central Coast and WCVI populations (Fig. 7). The observed response of these three populations to fishing over the last 20 years indicates that the expected and observed orders of resilience were similar except for the reversal between the WCVI and CC populations. We suspect that the WCVI population has been less resilient than the Central Coast population since 1988 either because: 1) it has exported more individuals, primarily to the GS population, than it receives, or 2) the GS population has been exporting less individuals to the WCVI than expected, or 3) both of the above. This could explain why the generally positive correlation in the spawner biomass of these two populations reversed and became negative in the 1990s. During this period, the WCVI population declined by about 30 kt, while the GS population increased by roughly the same amount (Schweigert 2001). Concurrently, water temperatures were above average and were punctuated by two strong warm ENSO events in 1991/92, and 1997/98. The 1991/92 event decreased the biomass and productivity of the euphausiid stocks in the region that herring juveniles and adults forage on (Tanasichuk 1998). Hence poorer feeding conditions may have altered the dispersal rates between the WCVI and GS populations from the expected pattern.

This possibility highlights the fact that dispersal is a complex process. And that it almost certainly responds to year-to-year and lower frequency changes in environmental conditions, and other factors that we don’t understand yet. Hopefully, the information that will emerge from the new coded wire tagging program will identify other important factors that modify dispersal rates between B.C. herring populations, and can be used to test the veracity of the density- and distance-dependent dispersal relationships described in this paper.

CONCLUSIONS

1. Dispersal rates from the five major populations during the cool base period (1951-76) ranged from 2% to 26% per year, and are significantly lower than the warm regime (1977-98) dispersal rates (range =15% to 36%).

2. Warm period dispersal rates increased with the spawner biomass in all populations. During the cool period, in two of the three cases with a reasonable contrast in spawner biomass, the dispersal rates also appeared to be density-dependent, with higher dispersal occurring at

higher spawner biomasses. In addition to this "density effect" there may also be a "regime effect", where the dispersal rates for a given spawner biomass tend to be slightly lower during cool climate regimes. However, more data are required to test this possibility.

3. A common *isolation by distance* relationship appears to describe the dispersal pattern during both cool and warm regimes. This relationship indicates that most herring stray to nearby populations. However, a few individuals stray to the most distant ones. Consequently, all of the major BC herring populations are genetically linked by dispersal, and the dispersal rates are high enough to ensure that there is unlikely to be any genetic differentiation between them. However, there could be some differentiation in some minor herring populations, which are more geographically or reproductively isolated from the major migratory stocks.

4. Dispersal-adjusted estimates of the average natural mortality rates (M_j) during the cool regime ranged from 0.16 to 0.52. There is a 92% probability that these rates are *lower* than the estimated warm regime natural mortality rates, which ranged from 0.33 to 0.61.

5. Average recruitment was significantly higher in the WCVI and QCI populations during the cool regime. It was also higher in the other populations, but the interannual variability was so large that much longer time series are required to determine if the apparent differences in these other populations are real.

6. Cool period spawner-recruit (S-R) relationships for the WCVI, GS, CC and QCI populations were dome-shaped. In contrast, the PRD S-R relationship fit a hockey stick model. The shape of the underlying S-R relationship was reversed during the warm regime.

7. The net dispersal rate time series output by the metapopulation model indicate that the Georgia Strait and PRD populations tend to be major exporters of adult herring to other populations, while the Central Coast and QCI populations are primarily importers. The net dispersal time series also suggest that seven large dispersal waves probably occurred in the metapopulation between 1951-1998.

8. Dispersal is important because it tends to stabilize the spatial distribution of spawners in the metapopulation; and increases the persistence time of the less productive populations in two ways: 1) the density-dependent dispersal response increases the fidelity rate when a population is declining, and (2) declining populations tend to receive more migrants from other populations than they export. Dispersal is also important because it recolonizes new and vacant spawning habitat. This enables the metapopulation to adapt to habitat changes, and to alter its spatial distribution in response to low frequency trends in climate, and other factors.

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APPENDIX

1. Natural Mortality Rate Adjusted for Dispersal.

The population-specific natural mortality rates (ASM-M_j) estimated by the age-structured model are actually *net loss rates*, which include real natural mortality plus the "hidden" effects of immigration and emigration (Ware and Schweigert 2001). Therefore, we calculated an adjusted-M (M_j) to account for the dispersal from, and to, each population. For mass balance, it follows that the PFB_j at the end of year *t* is equal to the recruiting biomass of fish, plus the biomass of repeat spawners ($RS_{j,t}$) plus the imported biomass ($IMPORT_{j,t}$) of mature fish in year *t*. Thus,

$$PFB_{j,t} = [Availability_j * Pre\text{-}recruits_{j,t}] + (RS_{j,t} + IMPORT_{j,t})_{final} \qquad \textbf{3.}$$

We calculated the average, initial biomass of repeat spawners and imported adults during the base period $(RS_{j,t}+IMPORT_{j,t})_{initial}$ from the age-structured model output and the estimated dispersal rates. The biomass of repeat spawners and imported adults $(RS_{j,t} + IMPORT_{j,t})_{final}$ at the end of year *t* after all the growth and natural mortality has occurred is given by:

$$(RS_{j,t}+IMPORT_{j,t})_{final} = (RS_{j,t}+IMPORT_{j,t})_{initial} \, EXP(G_j-M_j) \qquad \textbf{4.}$$

Equation 4 can be rearranged to yield a dispersal-adjusted natural mortality rate (M_j):

$$M_j = \ln [(RS_{j,k} + IMPORT_{j,k})_{final} / (RS_{j,k}+IMPORT_{j,k})_{initial}] - G_j \qquad \textbf{5.}$$

2. **Spawner-recruit Relationships.** It is recognized that analyses of spawner-recruit data are affected by measurement error. In general, Quinn and Deriso (1999) found that measurement error weakens the amount of density dependence (b) estimated by the Ricker model and reduces its statistical significance. On the other hand, there is little change in the estimate of "a". Consequently, since herring spawner biomass and recruitment are measured with error the density dependence estimates summarized below are underestimates; and the rather low R values are to be expected in the face of measurement and process error.

Table A1. Estimated stock-recruitment parameters for the three models for the cool base period. In this table, TSB indicates the smallest spawner biomass that produces maximum recruitment (maximum PRB).

Stock	Function	R	Threshold SB (TSB, kt)	Maximum PRB (kt)
WCVI	Ricker: PRB = 2.40SB EXP(-0.027 SB)	0.33	36	33
	Ware: PRB=1/((0.16EXP(0.025SB)/SB)+0.02)	**0.33**	36	31
	Hockey stick: If SB<20 Then (1.3SB) Else 26	0.27	>20	26
GS	Ricker: PRB = 3.64SB EXP(-0.032 SB)	0.53	31	42
	Ware: PRB=1/((0.86EXP(0.037SB)/SB)-0.066)	**0.59**	28	50
	Hockey Stick: If SB<20 Then (2.0SB) Else 42.4	0.52	>20	42
CC	Ricker: PRB = 3.50SB EXP(-0.077 SB)	0.26	13	17
	Ware: PRB=1/((0.23EXP(0.072SB)/SB)+0.016)	**0.27**	14	16

	Hockey stick: If SB<10 Then (1.45SB) Else 14.5	0.24	>10	15
QCI	Ricker: PRB = 2.22SB EXP(-0.055SB)	0.26	15	20
	Ware: PRB=1/((0.15EXP(0.065SB)/SB)+0.03)	**0.28**	16	18
	Hockey stick: If SB<11 Then (1.3SB) Else 14.3	0.19	>11	14
PRD	Ricker: PRB = 1.27SB EXP(-0.043SB)	0.25	23*	11*
	Ware: PRB=1/((cEXP(dSB)/SB)+f)	*	*	*
	Hockey stick: If SB<25 Then (0.93SB) Else 23.3	**0.39**	>25	23

* Model parameters are poorly determined.

Table A2. Estimated stock-recruitment parameters for the warm climate period. In this table, TSB indicates the smallest spawner biomass that produces maximum recruitment (maximum PRB).

Stock	Function	R	Threshold SB (TSB, kt)	Maximum PRB (kt)
WCVI	Hockey stick: If SB<20 Then (0.70SB) Else 14	**.**	>20	14
GS	Hockey stick: If SB<20 Then (1.45SB) Else 29	**.**	>20	29
CC	Hockey stick: If SB<18 Then (0.63SB) Else 12	**.**	>18	12
QCI	Hockey stick: If SB<18 Then (0.52SB) Else 9	**.**	>18	9
PRD	Ricker: PRB = 2.57SB EXP(-0.064SB)	**0.34**	16	15
	Ware: : PRB=1/((cEXP(dSB)/SB)+f)	*	*	14
	Hockey stick: If SB<15 Then (0.93SB) Else 14	0.22	>15	14

* Model parameters are poorly determined.

3. **Dispersal and the Stock Assessment Models.** We tested to see if the differences in the estimated spawner biomass between the Escapement and ASModels were positively correlated with the net dispersal rate time series (Fig.8). To test this possibility we calculated the difference between the Escapement and ASModel estimates of spawner biomass (SB_Diff = Esc_SB – ASM_SB; Schweigert 2001) for each population over the length of the time series (1951-98; Schweigert 2001). In an overly simplistic sense, the escapement model estimates (with error) the biomass that *"actually spawns" in year t*, while the ASModel estimates the biomass (also with error) that the model *"expects should return to spawn" in year t* (remember the ASModel assumes there is no dispersal). Consequently, we might anticipate a generally positive correlation between the SB difference and net dispersal time series. In this case, a negative difference in both time series implies that the population is exporting more biomass than it imports, while a positive difference implies that the population is a net importer of biomass. The following table summarizes the correlations between the SB difference and net dispersal time series.

Population	Correlation Coefficient [R]	Probability
WCVI	**+0.63**	**<0.0001**
PRD	**+0.46**	**0.001**

GS	-0.08	0.59
QCI	-0.12	0.41
CC	-0.12	0.40

There is a highly significant positive relationship between the two time series in the WCVI and PRD populations (Fig. 9). This implies that a significant proportion of the variation between the escapement and ASModel estimates of spawner biomass in these populations may be associated with dispersal.

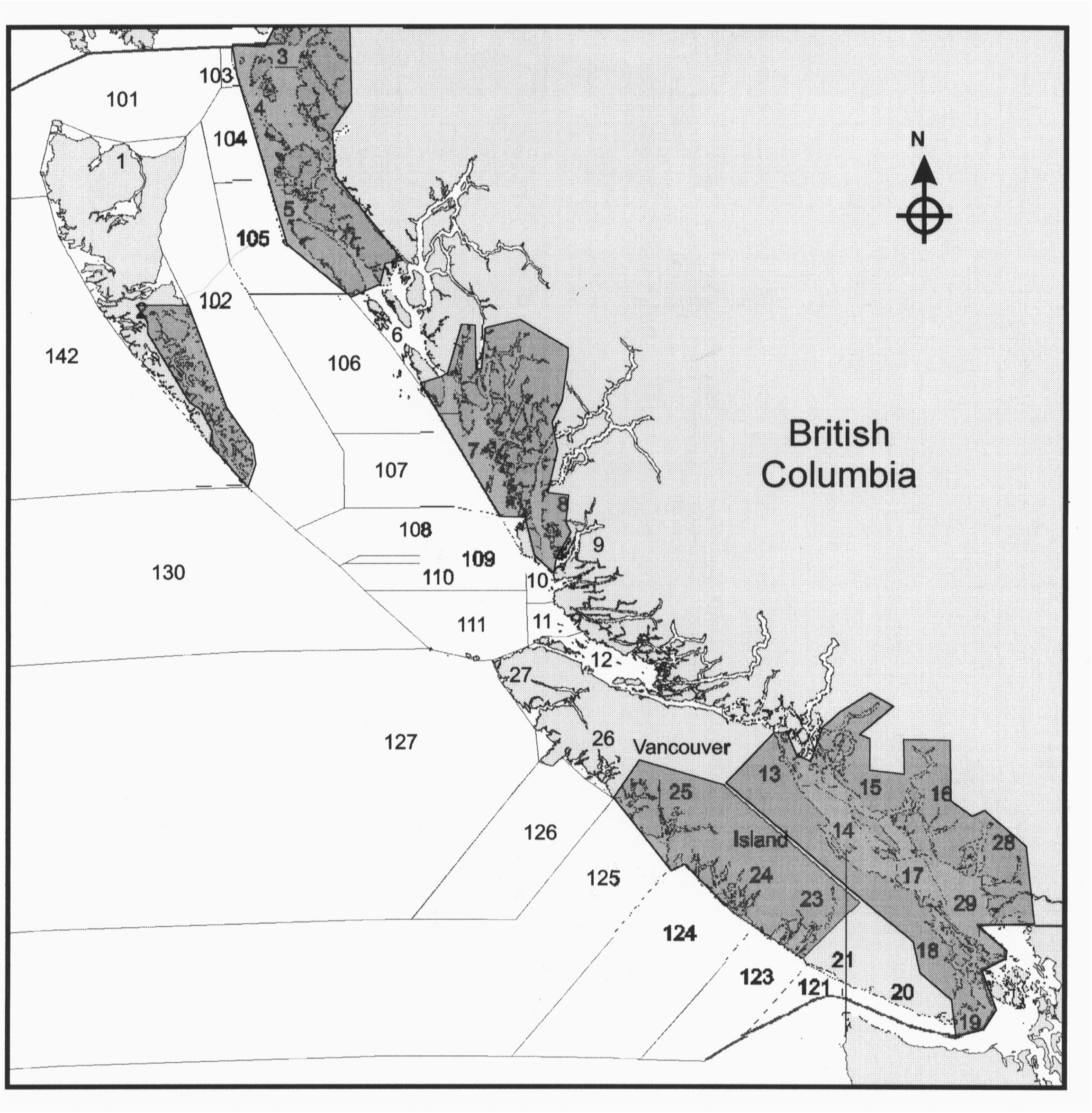


Figure 1. Locations of the five major, migratory herring populations in British Columbia. West Coast Vancouver Island (WCVI, includes statistical areas 23 to 25), Georgia Strait (GS, includes statistical areas 13 to 29), Central Coast (CC, includes statistical areas 7 to 9); Queen Charlotte Islands (QCI, includes the southeast coast of QCI), Prince Rupert District (PRD, includes statistical areas 3 to 5).

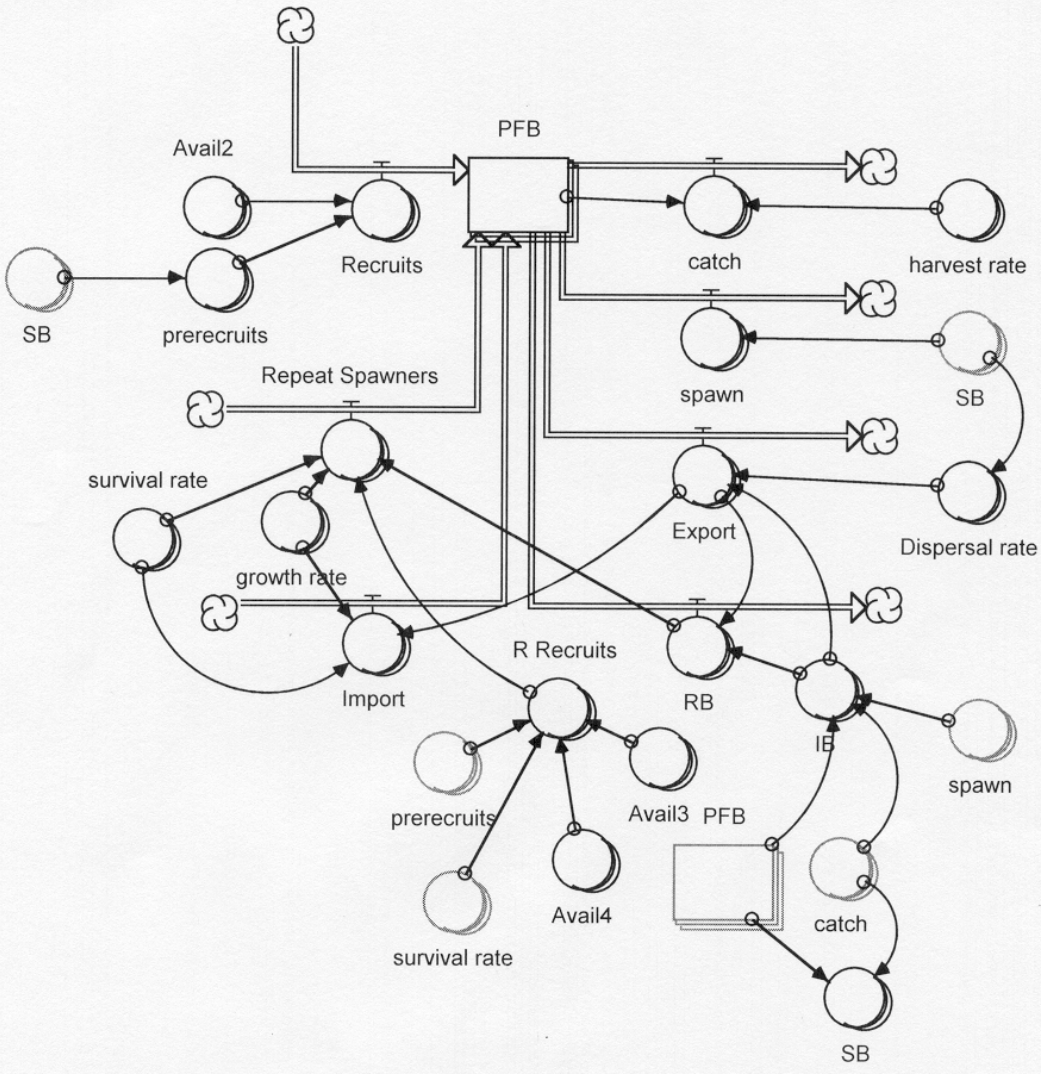


Figure 2. Structured metapopulation model. See text for a description of the variables and process equations.

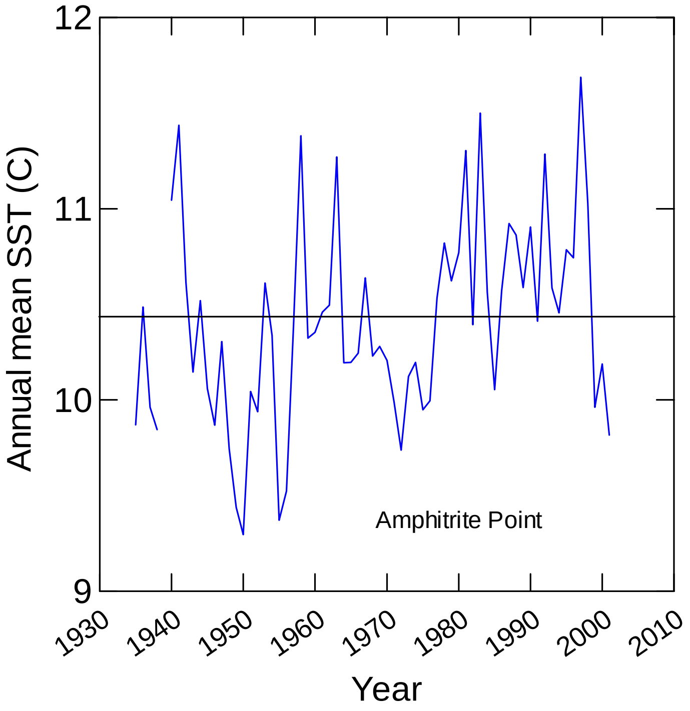


Figure 3. Annual sea surface temperature (^{0}C) time series for southwestern British Columbia. The horizontal line indicates the long-term mean temperature. The 1945-76 “cool” regime is apparent as a protracted period of negative temperature anomalies, punctuated by five scattered years with positive anomalies. The 1977-98 “warm” regime was a protracted period of positive temperature anomalies, with only two negative anomalies (in 1982 and 1985). Another regime change toward a cooler climate appears to have occurred in 1999.

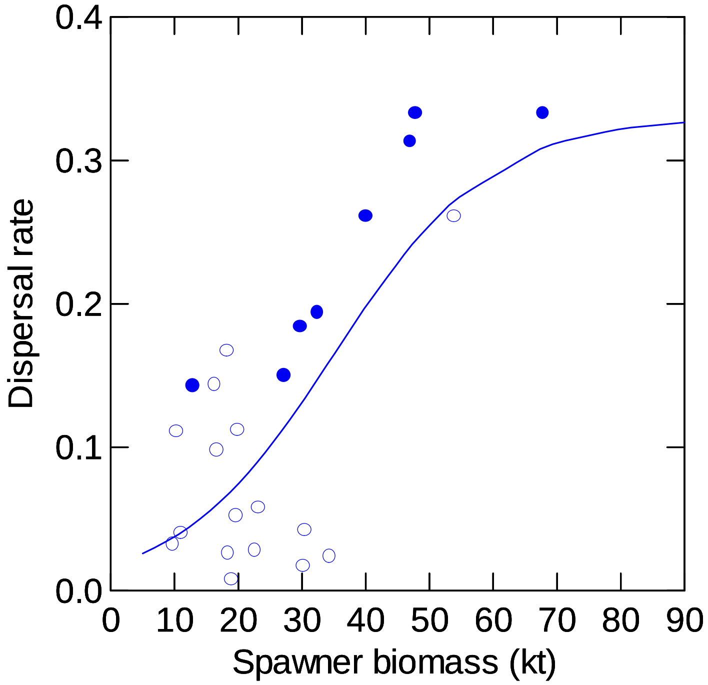


Figure 4. Common density-dependent dispersal relationship (solid line) obtained by combining the 1950s (open circles) and 1980s data (solid circles).

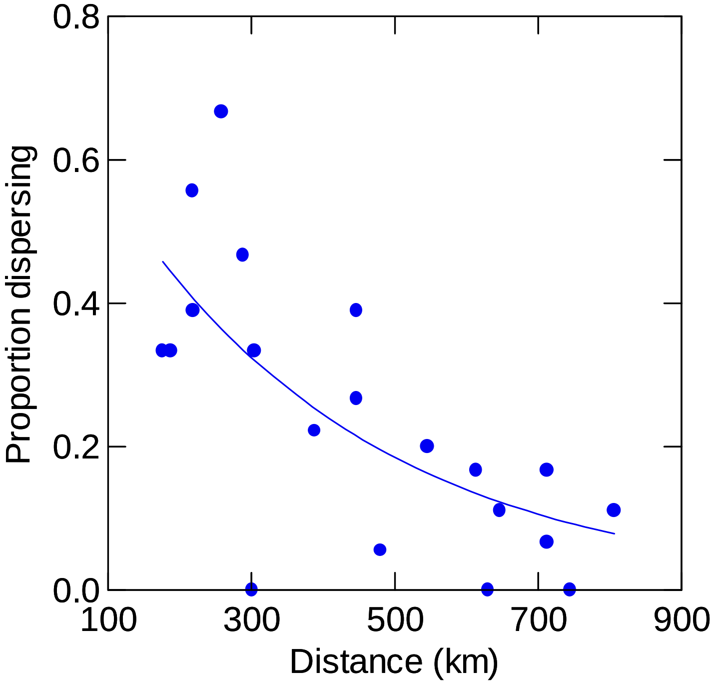


Figure 5. Isolation by distance relationship during the 1980s warm regime. The points indicate the proportion of herring dispersing to other populations during one year at large as a function of the distance between the source and destination populations. The data indicate that roughly 41% of the herring that dispersed were recovered a year later in adjacent populations that are about 200 km away; while about 10% dispersed to the most distant populations, which are about 700-800 km away.

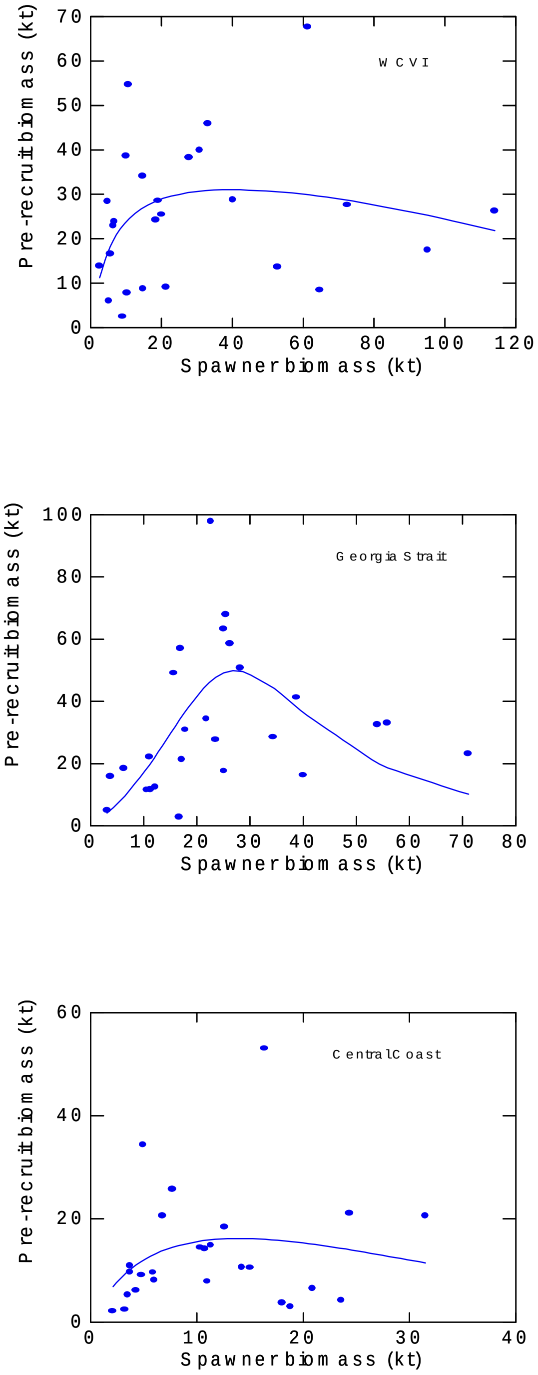
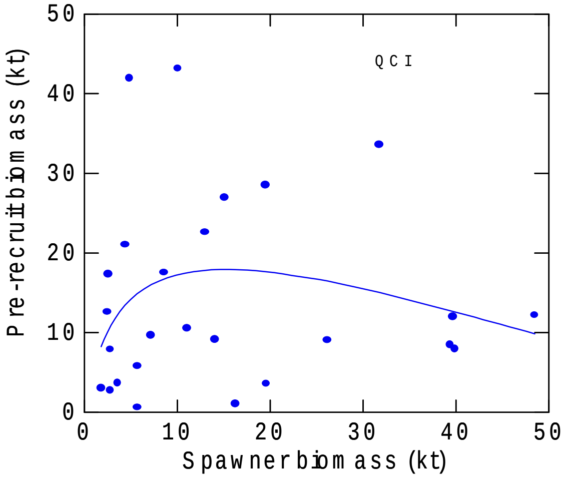


Figure 6. Stock-recruit relationships during the 1951-76 cool regime.



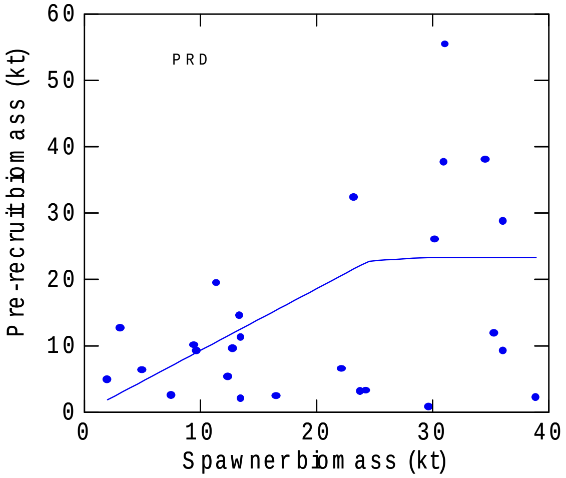


Figure 6 (cont.). Stock-recruit relationships during the 1951-76 cool regime.

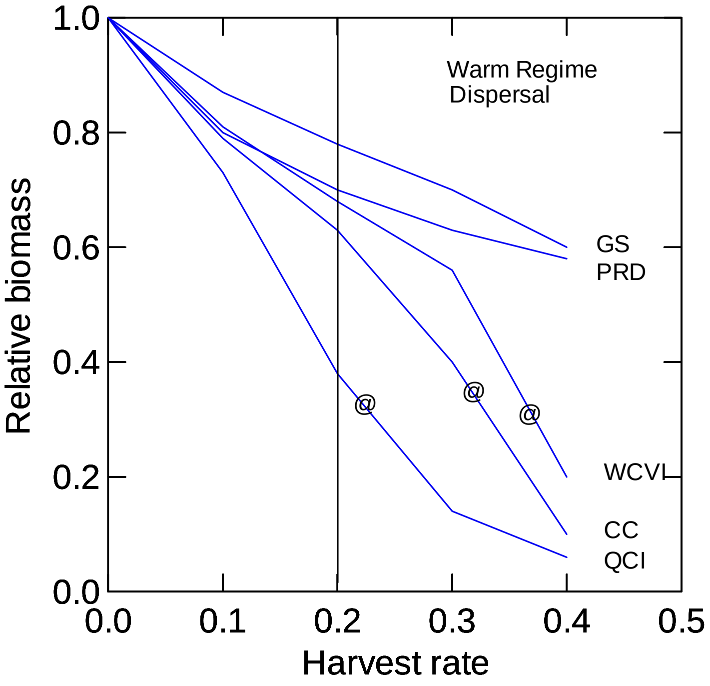


Figure 7. Theoretical decline in population biomass (relative to the warm regime carrying capacity) at different target harvest rates. The @ symbol indicates the estimated harvest rates for the QCI, CC and WCVI populations that will reduce the populations to their respective Cutoffs. The corresponding values for the PRD and GS populations occur at harvest rates >0.5 and therefore are not shown.

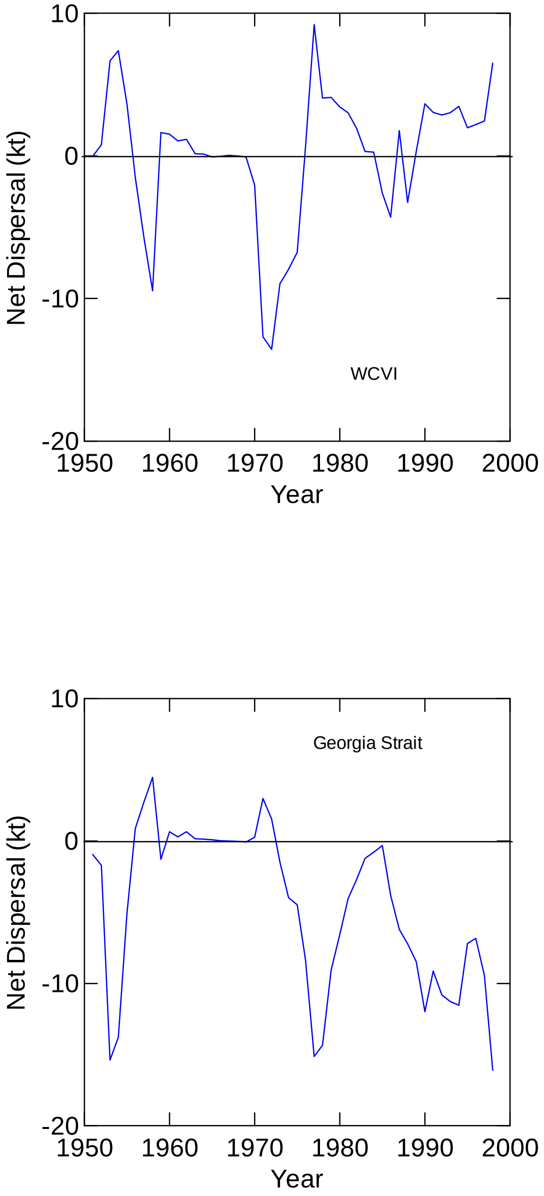


Figure 8. Net dispersal rate time series (kt/year) were calculated for each population by subtracting the exported biomass from the imported biomass in each year. Hence, a positive net dispersal rate indicates that the population imported more biomass than it exported, while a negative rate indicates that the population exported more biomass than it imported.

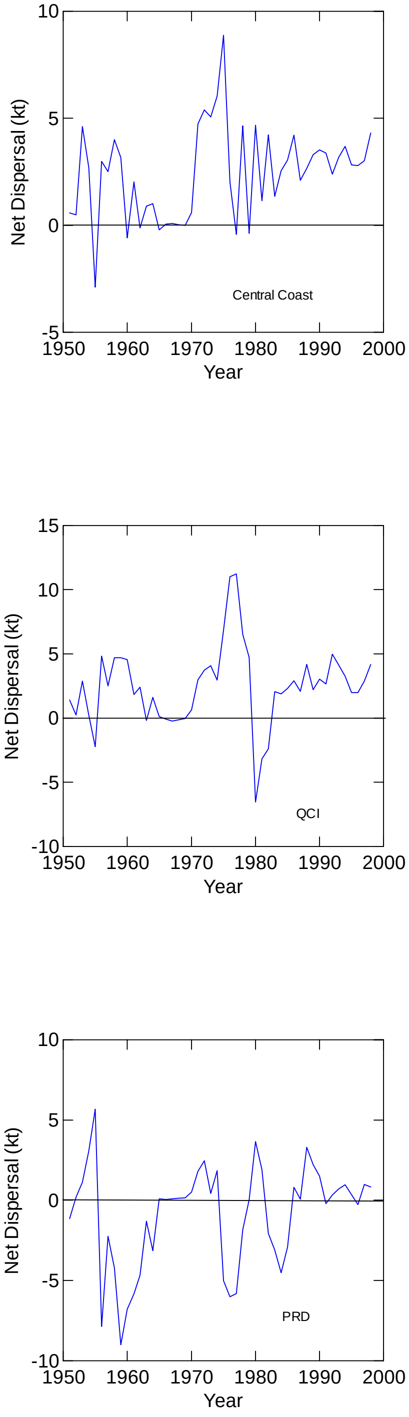
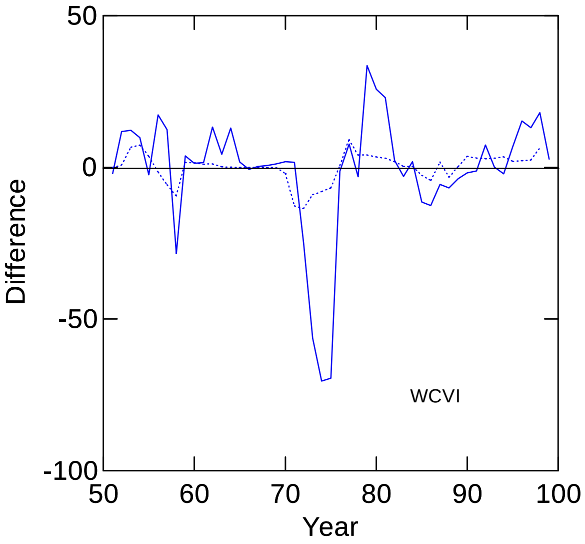


Fig. 8 (cont.) Net dispersal rate (kt/yr) time series for the northern populations.



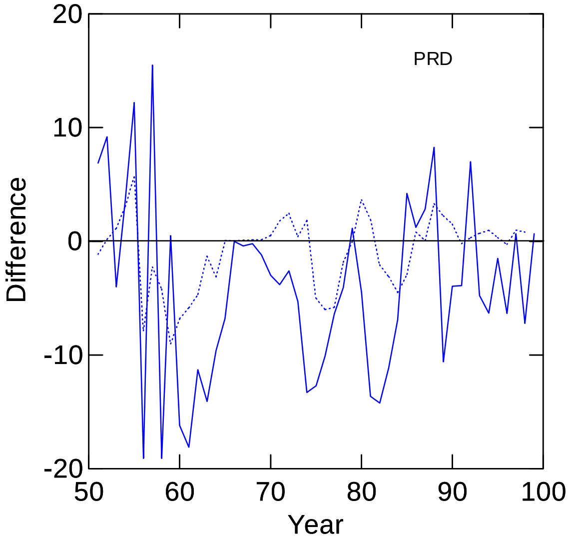


Figure 9. The solid line indicates the difference between the escapement and age structured model estimates of spawner biomass (*SB difference*). The dashed line indicates the net dispersal rate estimated by the metpopulation model (Fig. 8). These two time series are significantly correlated, which implies that differences in spawner biomass estimated by the two assessment models in these populations appear to be related to dispersal (see Appendix 3).