



Geographic variation in North Pacific herring populations: Pan-Pacific comparisons and implications for climate change impacts

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ABSTRACT

We review age-specific growth, recruitment, and population diversity of herring (*Clupea pallasii*) in the North Pacific. Eastern Pacific herring are smaller, grow slower, and reach a lower asymptotic weight (W_{∞}) than western Pacific herring. In the eastern Pacific, there are latitudinal differences in size but this variation is slight compared to east–west differences. The east–west growth differences match geographic patterns of genetic variation between eastern and western Pacific herring described in earlier reports. Both the genetic studies and the growth variation show that virtually all western Pacific herring populations, including those in the Bering Sea, cluster in one group, and all eastern Pacific herring, from the Gulf of Alaska to California, cluster in a second group. Population diversity, estimated as the number of separate populations per degree of latitude, is highest in the mid-ranges (latitudes) of herring distribution but the available supporting data are limited. Recruitment variation, examined by comparing the coefficient of recruitment variation for nine eastern Pacific herring populations, was highest in the Gulf of Alaska and lowest in southern populations. We suggest that the broad geographic differences in herring populations are adaptive, evolving in response to local prey resources, competitive and climate regimes. If so, examination of these differences can provide insight about potential effects of future climate change.

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1. Introduction

A special PICES/GLOBEC symposium was held in Honolulu, April 2006, to develop ‘basin scale syntheses’ of biological and oceanographic processes that affect the North Pacific, and to consider the impact of climate variability on those processes. This paper attempts to synthesize relevant biological information about Pacific herring (*Clupea pallasii*) populations.

Pacific herring have a wide distribution distinguished by a number of distinct populations. The biological differentiation of these populations is established (Blaxter, 1985; Haegele and Schweigert, 1985; Hay, 1985; Hay et al., 2001) but there has been no attempt to develop a synthesis of all populations in the North Pacific. Most definitions of ‘synthesis’ explain that the union of distinct components into a single aggregate can provide new or different perspectives that were not accessible from examination of the separate parts. The objective of this paper is to provide a synthesis of fundamental properties of herring populations in the North Pacific. The rationale is that such a synthesis may provide new insights about herring populations and factors affecting their variability, espe-

cially variability related to climate fluctuations. The key biological factors that we examine relative to geographic variation are growth (or geographic variation in size-at-age), spawning time and duration of the spawning period within a year, recruitment, and population diversity.

The Pacific herring is a relatively abundant forage species that occurs in the waters of all member countries of PICES. The species extends over broad ranges on both sides of the Pacific, mainly in shelf waters (<200 m depth), from nearly sub-tropical latitudes (<35° North) to Arctic waters (>70° North) (Hay and McCarter, 1997b). Herring populations vary in size from less than one thousand tonnes, equivalent to 10 million individuals weighing 100 g each, to several million tonnes, equivalent to 10 billion or more individuals (Hay et al., 2001; Stout et al., 2001; Gustafson et al., 2006). Pacific herring spawn exclusively in the ‘spring’ (late winter to early summer), unlike Atlantic herring (*Clupea harengus*) that have both spring and fall spawning populations (Blaxter, 1985). Like most marine fishes in temperate areas, the timing of Pacific herring spawning is earlier in the south and is progressively later in higher latitudes (Hay, 1985; Gustafson et al., 2006). Eggs are demersal, deposited in inter-tidal or shallow sub-tidal areas. Eggs hatch in 2–3 weeks and larvae are planktonic. After a pre-metamorphosis stage of 30–60 days, larvae develop into juveniles and

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reside mainly in nearshore habitats. The juvenile stage lasts approximately 2–3 years, ending with the onset of sexual maturity. The age of sexual maturity varies with latitude, and is youngest in the south (California) at 2 years and older in the north at 3–5 years (Bering Sea) (Barton and Wespestad, 1980; Hay, 1985). Differences in growth, reproductive variables, recruitment variability, and diversity among populations can provide increased understanding of how these populations may respond to climate variability.

2. Methods and materials

The objective of this paper, to synthesize information from many different populations, has forced us to compress a substantial volume of primary and grey scientific literature and data on North Pacific herring. This compression has required that some estimates are only approximations that cannot be determined with greater precision at the present time. For instance, usually there are significant differences in the way that different jurisdictions and agencies collect and summarize biological data, especially size and age data. For example, herring ages are measured in units of years but this requires that herring have birthdays, or a date when herring are classified as a year older than they were on the previous day. Such dates are arbitrary (i.e., the birthday of Canadian herring is set at July 1), and the convention used varies among agencies. Such variation in protocols for estimation of population parameters (such as age and measurement protocols) can confound attempts to distinguish between population differences arising from protocol differences versus ecological or climate-induced variation. Therefore the focus of this paper is one of generality and not 'precision'. We acknowledge that in the interest of brevity, there may be some fine-scale temporal and geographic differences among populations that we do not consider.

2.1. Growth: Size-at-age and fecundity data

Data used were from both published and unpublished sources. Data for British Columbia herring populations were extracted from databases maintained by Fisheries and Oceans Canada at the Pacific Biological Station, Nanaimo. These data on size (length and weight) at age are collected annually in support of annual biomass and fishery stock assessments and for other research. For all other herring populations, we used data from three sources: (1) data summaries provided by authors for use in the Wakefield herring symposium in 2000 (Hay et al., 2001); (2) data provided by scientists from several countries participating in a special PICES-GLOBEC symposium on size-at-age, held during the 2001 PICES annual meeting in Victoria, BC (PICES, 2001); and (3) data provided to PICES- and GLOBEC-sponsored workshops to develop trophodynamic models (Megrey et al., 2007) that relate climate and lower trophic level variation to herring growth.

For most populations included in this paper, the estimates of mean length-at-age and mean weight-at-age were based on data pooled over many years (usually more than 10) representing thousands of individuals for each sampling area. For various combinations of populations, we compared the mean age-specific length and weight, annual estimates of mean length at age-5, and asymptotic weight (W_{∞}). Following general methods described by Ricker (1975), W_{∞} was estimated using linear regression of annual age-specific increments (ASI) of weight (g) as the dependent variable versus the mean age-specific weight as the independent variable. The ordinate intercept (when the ASI was zero) was used as an estimate of W_{∞} .

A problem with comparing lengths at age among populations is the different or inconsistent reporting of length estimation among

various research or monitoring agencies. Some agencies use fork length and others, such as Fisheries and Oceans Canada, use total or standard length. Comparison of different measurement metrics can be misleading and obscure real geographic differences. Also, it is cumbersome to compare size-at-age for many different ages among many populations. The use of a single parameter (W_{∞}) avoids the problem with inconsistent length estimation. The estimates of W_{∞} were not normally distributed so the differences between the two sides of the Pacific were examined by a non-parametric Mann–Whitney test.

Size or age-specific fecundity data were available for five areas of British Columbia populations and three areas in Alaska. Relative fecundity (eggs/g) was calculated by dividing the total egg count by the whole body weight (soma and ovaries) of spawning females.

2.2. Recruitment data

Time series of annual recruitment were available from catch-at-age analyses from a total of nine herring populations (five in British Columbia and four in Alaska). British Columbia data are available in annual assessment reports (i.e., Schweigert and Haist, 2007). Data from Alaska populations were provided by Dr. Fritz Funk in support of PICES workshops (Funk, 2001). For each population, recruitment variation was estimated as the coefficient of variation of the logarithm of annual recruitment (CVR = mean/SD) based on the time series of annual recruitment data. Recruitment data from the Hokkaido-Sakhalin herring population in the western Pacific were from Nagasawa (2001), who provided numbers-at-age data for the Hokkaido-Sakhalin herring catch from 1907 to 1957. We used Nagasawa's estimate of the annual number of age-5 herring as an indicator of the temporal pattern of recruitment. This stock collapsed in the 1950s, so subsequent estimates of annual recruitment were not available.

Mertz and Myers (1994) hypothesized that recruitment variability of marine fish species should decrease as the duration of the spawning period increased. Hay (1985, Fig. 10) showed that spawning was later and that the duration of the spawning period was shorter at high latitudes. The duration of spawning is the difference in time between the beginning and end of the annual spawning period for each population. We tested the Mertz and Myers hypothesis by comparing the CVR by latitude of each population. If the Mertz and Myers hypothesis is valid for herring, we would expect the CVR to increase in higher latitude populations. Accordingly we estimated the approximate latitude for nine populations for which the CVR was estimated, and compared this with the estimated CVR for each population.

2.3. Herring population diversity

A detailed review of the Washington State Cherry Point herring population (Stout et al., 2001; Gustafson et al., 2006) provided useful lists of putative Pacific herring populations for all of the United States from California, Oregon, Washington, and Alaska. These lists were used for this paper. The list of herring populations for Canadian (British Columbia) herring areas was adapted from previous reports of herring populations (Taylor, 1964; Hay and McCarter, 1997a), and from more detailed technical reviews (Hay et al., 1989). We also examined the number of distinct populations per degree of latitude and number of populations per unit of coastline in different regions for the eastern Pacific. Population diversity may be related to the complexity of the coastline, with more complex coastlines able to support more populations. Regions were defined as: Bering Sea, Alaska Gulf, southeastern Alaska, north British Columbia, south British Columbia, Washington, Oregon, and California. Corresponding information was not available

for the western Pacific so our understanding of population diversity there is speculative.

Distances of coastlines by region were estimated using Arcview Spatial Analysis © applied to basemaps of the Canadian and US coasts with spatial resolution of about 1 km. A basemap of the US coastline was provided by the National Weather Service (http://www.nws.noaa.gov/geodata/catalog/national/html/us_state.htm). The British Columbia coast basemap was developed by the Canadian Hydrographic Service. All estimates of coastal distances were made in kms. The regional estimates are approximate because of irregularities in regional boundaries. For instance, for simplicity in this analysis we distinguished between the coast of British Columbia and Alaska as simply north or south of 55° latitude, but the actual boundary separating northern British Columbia and Alaska is more complex. The error related to this approximation is very small relative to the differences in total coastline among regions.

2.4. Data analyses

Length at age 5 was compared among 10 eastern Pacific and one Bering Sea herring population (Table 1) using a one-way ANOVA (Minitab Statistical Software©). The mean annual lengths at age 5 for the 11 different populations, which spanned from California to the Bering Sea, were compared on a simple plot. Length at age, from ages 2–14, were compared for seven representative populations: two from the western Pacific (Hokkaido-Sakhalin and Yellow Sea herring), one from the Bering Sea, and four from eastern Pacific populations (California at SF Bay, the west coast of Vancouver Island, the Prince Rupert District in northern BC, and Prince William Sound in the Gulf of Alaska). The estimated asymptotic weight (W_{∞}) for each population was compared by a non-parametric Mann–Whitney test (Minitab Statistical Software©). The coefficient of variation of recruitment (CVR) was estimated from the estimated numbers of age 3 herring in three Alaskan populations and five BC populations. The CVR for the Bering Sea population was estimated from the numbers of age 4 herring. A north–south trend in the CVR was compared by linear regression (Minitab Statistical Software©). Variation in recruitment of the Hokkaido-Sakhalin herring population was estimated from the numbers of age 5 fish (in millions) by year class from data presented by Nagasawa (2001).

3. Results

3.1. Geographic variation in growth and fecundity

Inter-annual variation in herring length at age-5 in the eastern Pacific was relatively small from California to the Gulf of Alaska,

but Bering Sea (Togiak) herring were substantially larger than the more southern populations in the eastern Pacific (Fig. 1a). The differences in length at age-5 between Bering Sea herring and those in the eastern Pacific, examined by one-way ANOVA, were highly significant ($p \ll 0.001$, 10 df). Lengths of western Pacific herring were longer at all ages than eastern populations (Fig. 1b). Lengths of Bering Sea herring were intermediate between the eastern Pacific (California to the Gulf of Alaska) and the western Pacific populations. When estimates of W_{∞} were compared over the entire North Pacific, it was clear that herring in the western Pacific achieved much greater weights than eastern Pacific populations (Fig. 2). The east–west difference in W_{∞} , examined by a non-parametric Mann–Whitney test, was significant ($p = 0.0034$).

The geographic patterns of asymptotic weight (W_{∞}) showed that eastern Bering Sea herring clustered with the western Pacific herring populations (Fig. 2). All western Pacific herring populations had a much heavier W_{∞} than eastern Pacific herring (California to the Gulf of Alaska). All eastern Pacific herring populations clustered as a different group, with W_{∞} generally increasing with latitude (143 g in California to ≥ 278 in Alaska, Fig. 2).

3.2. Population diversity

Within the eastern Pacific, the degree of population structure varies with latitude: the greatest number of distinct populations (or ‘populations per degree of latitude’) occurs in the center of the range (Washington State and British Columbia) and the least occurs at the extremes (California and the Bering Sea) (Table 2). Although it may be difficult to get consensus among researchers about the exact population configuration (or populations) in any area, there clearly is higher population diversity in the mid-latitude regions (British Columbia and Washington State).

For the eastern Pacific, there appears to be a higher population diversity per unit coastline (i.e., 1000 km segments) in the southern part of the range with >4 populations/1000 km coastline in California and $<0.4/1000$ km of coastline in all northern regions (Table 2). It is not clear, however, if there is any biological significance to the apparently greater diversity in southern latitudes. That aside, these analyses show that the population diversity is not simply a function of coastline complexity because the relatively straight or simple coastlines of California, Oregon, and the outer coast of Washington State have a relatively large number of (small) populations. These populations appear to be associated with coastal estuaries, perhaps as locations that are suitable for spawning and incubation of early life stages (Hay and McCarter, 1997b).

Comparisons of population diversity between the eastern and western Pacific were more difficult because there is little relevant

Table 1

Location and data characteristics of herring populations in the Eastern Pacific and the Bering Sea (Togiak)

Location	Region	Latitude	Earliest	Latest	N
San Francisco Bay (SF Bay)	California	37	1973	1999	27
Tomales Bay	California	38	1979	1997	18
West Coast Vancouver Island (WCVI)	British Columbia	49	1950	2000	44
Strait of Georgia (GS)	British Columbia	50	1950	2000	44
Central Coast (CC)	British Columbia	52	1950	2000	45
Queen Charlotte Islands (QCI)	British Columbia	53	1950	2000	39
Prince Rupert District (PRD)	British Columbia	54	1950	2000	46
Sitka	Southeast Alaska	57	1943	2000	54
PWS	Gulf of Alaska	61	1941	2000	38
Kodiak	Gulf of Alaska	58	1980	1998	19
Togiak	Bering Sea	59	1981	2000	20

Mean length at age 5 were compared in Fig. 1, and W were compared in Fig. 2. The columns show the general location (Region) of each population, their approximate latitude, earliest and latest year of the length data, and the number of years examined (N).

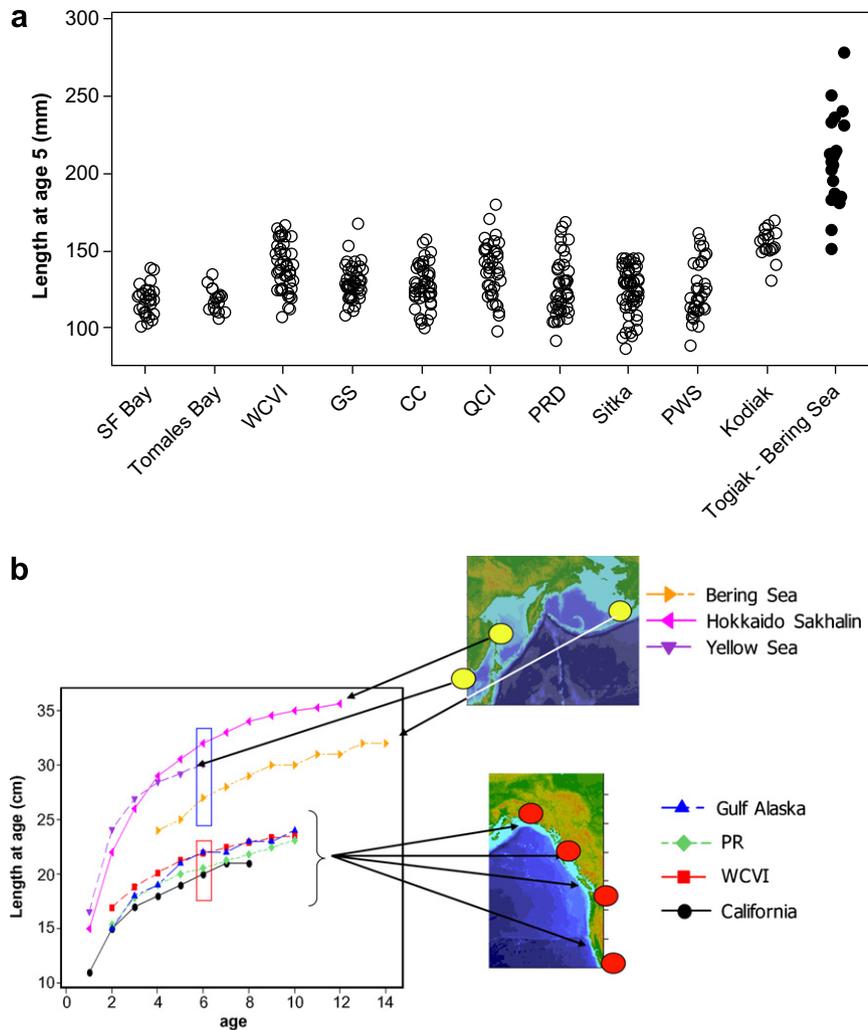


Fig. 1. (a) Comparison of length at age 5 for 10 eastern Pacific herring populations and one Bering Sea population (Togiak) arranged approximately by latitude, from south to north. The abbreviations of population name and latitude of each population are shown in Table 1. The Togiak herring (dark circles, extreme right) were almost always larger than the more southern herring. The differences, examined by ANOVA, were significant ($P \ll 0.001$). (b) Comparison of length-at-age for four eastern Pacific populations, Bering Sea herring, and two western Pacific herring populations. The similarities of length-at-age in the eastern Pacific can be seen by the cluster of points in the lower vertical box. In contrast, the Bering Sea and western Pacific herring cluster in the upper box. At a given age, western Pacific herring are larger than eastern Pacific herring and Bering Sea herring are intermediate.

literature for the western Pacific. Based on the data we were able to access, we tentatively concluded that there appeared to be a higher diversity of populations – or a greater number of smaller populations – in the eastern Pacific compared to the western Pacific (Fig. 2; Table 2). Our analysis is tentative, however, because much more attention has been placed on stock identification on the eastern side of the Pacific.

3.3. Area-specific recruitment and the duration of spawning season

When the coefficient of variation of annual recruitment (CVR) was compared to the latitude of each population, the northern Alaskan populations exhibited both the highest inter-annual variability within a population (highest CVRs) and the greatest range of variability among populations (Fig. 3). The variation in recruitment in the eastern Pacific appeared to be least in the south (British Columbia) and greatest at the northern edge. A linear regression of the CVR by degrees of latitude ($\text{CVR} = -15.7 + 0.332 \text{ latitude}$) had a positive slope and was significant ($P = 0.009$). However, we do not have data on recruitment variability for other, more southerly, populations.

4. Discussion

4.1. Increase in size with latitude – still unexplained

The positive correlation between asymptotic weight (W_{∞}) and latitude, that is very apparent in the eastern Pacific (Fig. 2), was expected. In species with broad geographic distributions, such as Pacific herring, most individuals in southern areas are smaller, with lower longevity and higher relative fecundity than fish from higher latitudes (Blaxter, 1985; Blaxter and Hunter, 1982). What is surprising is that there is no clear explanation for these latitudinal phenomena. Variation in growth with latitude is well known in poikilotherms in general (Lindsey, 1966), and in herring in particular (Blaxter, 1985; Hay, 1985). However, the biological explanation for these observed differences is less certain – and perhaps even paradoxical. The apparent contradiction is between the observations, made from many different ectothermal species, that early life-history growth is slower at cool temperatures, but that animals reared in such environments achieve larger body size as adults (Atkinson and Sibly, 1997). Our analyses showed herring also follow this contradictory pattern – with largest herring ob-

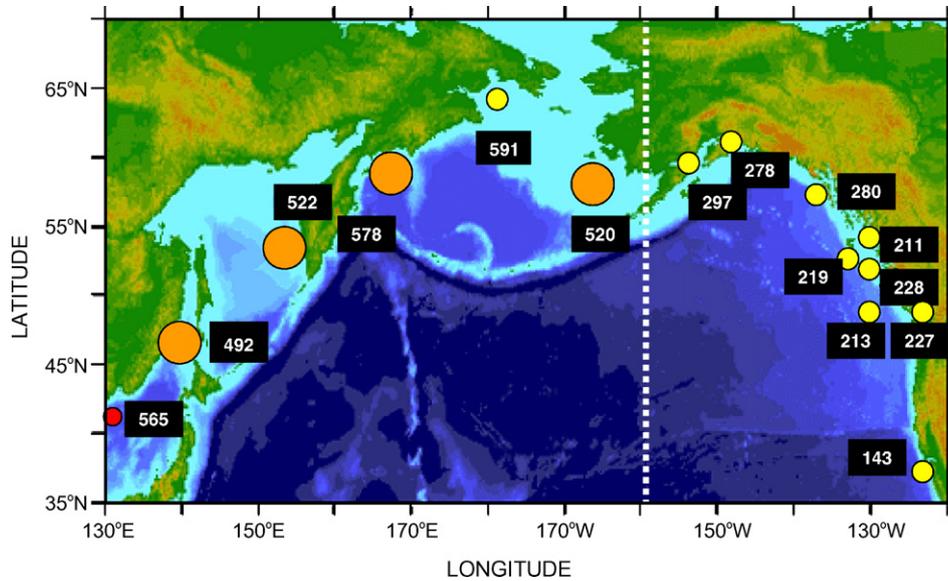


Fig. 2. Comparison of estimates of W_{∞} for herring populations in the North Pacific. The large circles represent populations that may sometimes exceed 1 million metric tonnes. Smaller circles represent smaller populations. The locations are approximate. The white vertical line separates eastern and western herring. The east–west difference in W_{∞} , compared by a non-parametric Mann–Whitney Test, was significant ($P < 0.01$). The map is adapted from a NOAA website: www.pmel.noaa.gov/np/pages/seas/npmap2.html.

Table 2

Population diversity in regions expressed as the number of herring populations (Pops) per degree of latitude (Pops./°L) and per 1000 km of coastline (Pops./km $\times 10^{-3}$)

Region	Min–max (°L)	Range (°L)	Pops.	Pops./°L	km	Pops./km $\times 10^{-3}$
Bering Sea	55–67	12	7	0.56	44,978	0.16
Alaska Gulf	57–61	3	6	2.00	60,214	0.10
Alaska SE	54–60	6	6	1.00	85,472	0.07
British Columbia (north)	51.5–54.5	3	8	2.60	23,867	0.34
British Columbia (south)	48.5–51.5	3	9	3.00	20,839	0.43
Washington	46–49	3	11	3.75	5543	1.98
Oregon	42–46	4	4	1.00	1214	3.29
California	32–42	10	15	1.50	3512	4.27

The minimum and maximum degrees of latitude (Min–max-°L), range of latitude, and km of coastline are also shown for each region.

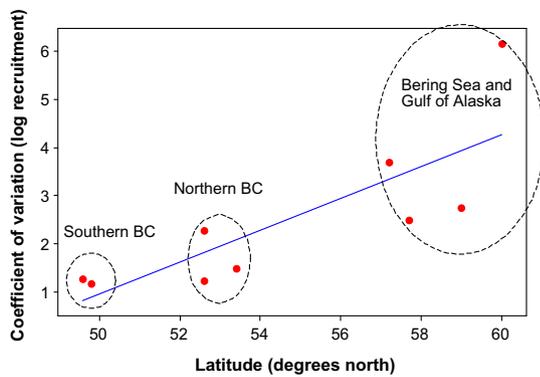


Fig. 3. The coefficient of variation of recruitment (CVR) for nine eastern Pacific herring populations shown as a function of latitude. Recruitment is defined here as the logarithm of the estimated number of age 3 herring (age 4 for the Bering Sea) entering the spawning population. A linear regression of the CVR by latitude was significant ($P = 0.009$), which supports the contention that populations at higher latitudes have greater variability in recruitment.

served at northern locations (Figs. 1 and 2). This phenomenon, when examined over a wide range of taxa, is independent of food resources and appears to be a physiological attribute of most organisms, but as Atkinson and Sibly (1997) point out, a general,

all-encompassing explanation is not available at the present time. They suggest that the solution may involve a fundamental relationship between developmental temperature and cell size. This topic is outside the scope of this paper but this unresolved puzzle has implications for ecological analyses of climate change impact because it is established that growth rate and body size influence many critical processes in fishes, such as maturity, fecundity, and mortality (Rose et al., 2001, 2008).

Most studies of fish populations that have undergone relatively large changes in their abundance invoke changes in size-at-age to help explain the population response (e.g., Shuter, 1990; Rose et al., 2001). This seems reasonable because fecundity and mortality must balance in order for populations to remain in equilibrium over the long term. We adapted data from Stout et al. (2001) (except for Alaska, for which we used size data reported in Funk, 2001), and computed eggs per gram (whole body weight per spawning female) by specific regions in the eastern Pacific. Relative fecundity was 220 eggs/g in California, 200 in British Columbia, and 150 in Alaska. Egg size also varies with fish size within areas; larger females have slightly larger eggs and there is some evidence that egg size may vary with latitude (Hay, 1985). The higher relative fecundity in southern females implies that we might expect to see latitudinal variation in growth and recruitment variability. Therefore, until we better understand the relationship between temperature, growth, and body size, there will be a limit to the

ability of predictive models developed for specific locations to provide general explanations of the impacts of climate change on a species like Pacific herring.

4.2. East–West differences in growth and asymptotic weight

An important aspect of the synthesis in this paper is the simple observation that herring growth rates are fundamentally different between the eastern and western side of the Pacific (Figs. 1 and 2). We acknowledge however, that the presentation in this paper is general, and there are likely exceptions on both sides of the Pacific. For instance, herring in Kotseby Bay (Sea of Okhotsk) have slow growth rates similar to eastern Pacific herring (N. Naumenko and V. Radchenko, unpublished data). Other populations, especially those that live in brackish lagoons in the western Pacific, also may have relatively low asymptotic weights, but such populations are small and somewhat rare, so it seems that most western Pacific herring populations have the potential for a high asymptotic weight. Conversely, there are occasional references made to undocumented reports of large herring ('giants') in British Columbia, and in other parts of the eastern Pacific, but there are no reports or data to confirm such suggestions. One ostensible population that was alleged to have exceptionally large fish was the 'Point Grey population', adjacent to the city of Vancouver, BC. Thompson (1916) provides length frequency data from herring captured from this area in 1916, a time preceding the development of intense industrial fisheries. The Point Grey herring were larger than herring taken in other areas of the Strait of Georgia, but only slightly, with a median length of about 22 cm and a maximum of about 26 cm (see Fig. 12, Thompson, 1916). Such length distributions may be slightly larger than those of adjacent areas but they are not exceptional. Similar lengths could be found in samples taken in recent years, and more importantly, these lengths are still substantially smaller than the sizes reported for western Pacific herring. These slight differences in size reported by Thompson (1916) may be the basis for misunderstandings about size variation in some populations, as they may become exaggerated over time. Therefore, it seems reasonable to conclude that, in general, western Pacific herring grow faster (Fig. 1) and larger (Fig. 2) than herring on the eastern Pacific side. To date, there does not appear to be any convincing evidence or data reports to indicate that any eastern Pacific herring grow as large as those in the western Pacific. The size difference between western and eastern herring is substantial, and much greater than the latitudinal differences within eastern Pacific herring from California to the Gulf of Alaska. The close resemblance of the geographic variation in growth (this paper) with two previous genetic analyses (Grant and Utter, 1984; Jørstad, 2004) indicates that these growth differences may have a genetic component.

The reasons for the east–west differences in growth and asymptotic size are uncertain. Presumably the differences reflect some fundamental differences in trophic ecology, but it is puzzling that the between-basin east–west differences exceed the within-basin north:south differences. Harrison et al. (1999) point out that primary productivity is similar between the eastern and western gyres in the north Pacific, although nutrients are slightly higher in the west. Mackas and Tsuda (1999) compare mesozooplankton between the eastern and western regions of the north Pacific. They tentatively conclude that the productivity may be higher in the western Pacific but comment that such variation occurs in the context of considerable intra- and inter-annual variation in both regions. Hay and McCarter (1997b) point out that maximal herring population size is positively related to the total area of the continental shelf area used by the population and in general, continental shelf areas in the western Pacific are much greater than those of the eastern Pacific. They also show that the herring density (g/m^2), estimated by dividing population biomass by the area of

continental shelf used by the population, is generally higher in the eastern Pacific, even among small populations. Therefore it seems that the east–west differences in asymptotic size are not easily explained by obvious differences in primary or secondary productivity, and that the body size of a herring is not directly related to its population size.

What are the implications of this distinct geographic difference in body size between the eastern and western Pacific? Probably the adaptation to dispense energy to somatic growth favors individuals that live longer with a lower annual reproductive output, but with a longer reproductive life. In contrast, the shorter-lived, more fecund herring in the eastern Pacific appear to maximize their reproductive output in a shorter life span. Such a strategy would require that eastern Pacific herring have relatively more opportunities for years producing successful cohorts.

4.3. Population diversity

The comparison of population diversity between the eastern and western Pacific is not fully resolved because of uncertainty about potential, but unreported, population differentiation in the west. However, it is likely that the general trend for a greater number of smaller populations in the east (Table 2) is reasonable because it seems that many of the habitats where herring reside in the western Pacific are subject to rapid and extreme climate fluctuation, especially in temperature. For instance, the Yellow Sea herring appear to be ephemeral, appearing at some periods and disappearing at other times, perhaps following natural variation in climate (hydrological) cycles (Hay et al., 2001; Tang, 1981). In the Sea of Okhotsk, annual variation in ice cover, both in terms of the geographic extent of ice and the duration of ice, changes the accessible spawning habitat of herring, perhaps over many hundreds of nautical miles (Tyurnin, 1973). Therefore, it may not be possible for most western Pacific herring populations, such as the Okhotsk herring, to differentiate into the relatively high degree of spatial structure seen in eastern Pacific herring.

4.4. Recruitment variation versus spawning duration

Myers (2001) reported evidence that recruitment variation was least in the mid-ranges of the marine fish populations. While it is clear that herring spawn earlier in southern areas, both in the eastern and western Pacific (Blaxter, 1985), the geographical variation in the duration of the spawning season is less clear. Most evidence suggests that spawning duration is shorter in the north (Hay, 1985). The examination of this hypothesis in Pacific herring in this paper was necessarily restricted to the eastern Pacific because data were not available for most western Pacific populations.

Assuming that southern BC populations represent herring that are approximately at the middle of their north–south range in the eastern Pacific, we found that recruitment variability increased with latitude (Fig. 3). Therefore, this simple analysis provides partial corroboration to the suggestion and model by Mertz and Myers (1994) that recruitment variability is related to spawning duration. The suggestion invokes the basic match–mismatch hypothesis (Cushing, 1990) as a factor controlling recruitment. Presumably populations with a longer spawning duration would have a higher probability of encountering peaks of zooplankton abundance. However, Stout et al. (2001) provide evidence indicating that the duration of spawning of eastern Pacific herring was greater in the middle parts of the range. They showed that populations in the mid-latitudes (British Columbia) have the longest spawning duration of any population on the Pacific coast. The summary by Stout et al. (2001) was based partially on earlier reports by Hay (1985) and others that reported on a range of spawning times of aggregated populations. These included some small, unique, late

spawning herring that are not represented in commercially fished populations. There are no time series data on recruitment for these small populations, and because different populations were aggregated in the Stout et al. (2001) summary, it is not clear if spawning duration of individual populations is appreciably longer in the middle of the range of eastern Pacific herring, such as in the British Columbia coast.

Recruitment time series are limited for most western Pacific herring populations and this limitation prevents examination of recruitment variability with latitude. A noteworthy exception is the long-term recruitment time series for the Hokkaido-Sakhalin population (Fig. 4). However, comparison of the Hokkaido-Sakhalin recruitment time series to the time series from the eastern Pacific is confounded by the unexplained decline in the Hokkaido-Sakhalin population. Prior to 1930 in the Hokkaido-Sakhalin herring population, there was a relatively high frequency of years with strong year classes. After 1930 there were only a few years of relatively strong recruitment. The explanation for the decline and failure to recover of the Hokkaido-Sakhalin herring population remains an enigma. This herring population did not rebound during the war period (1939–1945) when catches were much reduced. Based on Nagasawa's (2001) work, the simplest explanation for the decline is climate variation or climate change. Specifically, retrospective analyses showed that maintenance of high spawning biomass was dependent on the formation of strong year classes every few years. Within the 20th century, strong year classes were formed only in years with low sea surface temperature anomalies. Large catches of the Hokkaido-Sakhalin stock were supported by very strong year classes. Such strong year classes were produced during the low SST period in the 20th century. Low to near-average SST conditions were related to big catches during the early period of the 19th century and also to high CPUE's during the late 1870s to the 1880s. Very poor catches occurred during high SST periods. This explanation does not preclude the effect of over-fishing as the explanation for the decline, but another factor(s) must be preventing the recovery. Perhaps the lack of recovery, as seen in the steadily declining recruitment (Fig. 4) beginning in the 1930s and 1940s, represents the beginning of climate change impacts on western Pacific herring.

4.5. Climate change impacts

Climate change impacts may depend on population configuration. For instance, two of the other dominant clupeid populations in the northeast Pacific, the Pacific sardine (*Sardinops sagax*) and

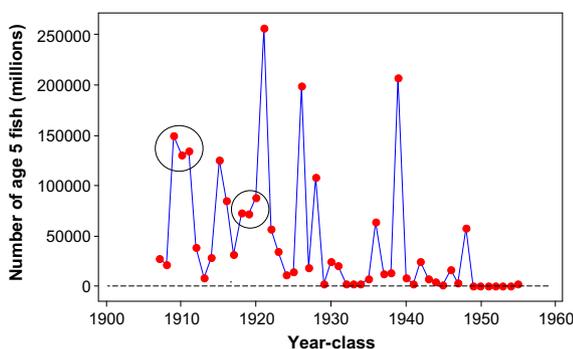


Fig. 4. Variation in recruitment of the Hokkaido-Sakhalin herring population as shown by the numbers of age 5 fish (in millions) by year class. Prior to 1930, there was a relatively high frequency of years with strong year classes, sometimes occurring in consecutive years (circles). After 1930, there were only a few years of relatively strong recruitment and most years had very low or no recruitment (indicated by points on the horizontal dotted line). The population has not recovered since the 1940s and 1950s. (Based on data presented by Nagasawa, 2001).

the northern anchovy (*Engraulis mordax*), can develop into large, genetically homogenous populations covering large geographic ranges (Hart, 1973). The exact range varies with annual climate variation, with more seasonal migrations and occupation of more northerly locations in warmer years. Therefore, for Pacific sardine and northern anchovy, it seems probable that one impact of climate change would be a change in range or the center of their geographic distributions. In contrast, eastern Pacific herring populations tend to differentiate into a relatively large number of smaller populations that seem to be more tightly linked to local geographical location. Herring populations, however, also seem to have a wide tolerance for inter-annual variation. At most latitudes between California and the Gulf of Alaska, there is a combination of large migratory populations that move from nearshore spawning areas to shelf waters to feed, and smaller, local populations that are confined mainly to inshore waters such as fjords, inlets and estuaries (i.e., Carlson, 1980; Hay and McCarter, 1997a; Gustafson et al., 2006). It seems probable that the local inshore environments may experience more climate variability so the smaller, non-migratory inshore populations may sometimes be closer to the limits of their ecological or physiological tolerance than the larger, migratory populations. If so, future climate change may have a greater impact on the smaller, nearshore populations than on the larger migratory populations, leading to a loss of population diversity. Over decadal scales, and especially in southern areas, this could lead to extirpation of peripheral populations, but it may also lead to the expansion of existing populations in the mid-ranges of the distribution and perhaps development of new populations in extreme northern areas.

A different (but not mutually exclusive) scenario for impact of climate change on herring is that, for much of their range and especially in the middle regions, eastern Pacific herring may be capable of a more flexible response to habitat and environmental change than western Pacific herring. There is more population diversity in eastern Pacific populations than in the western Pacific – but we acknowledge that this is not confirmed. If it is correct, however, and unless climate changes are substantial, we may not detect much impact on most eastern Pacific herring, especially the migratory populations. In the western Pacific, it appears that, within the latitudinal ranges occupied by herring, environmental conditions are more heterogeneous and perhaps more extreme. For instance, during much of the year, the difference in temperature extremes between California and the Gulf of Alaska is relatively small in contrast to those between the Yellow Sea or East China Sea (the southern end of the range of western Pacific herring) and the Sea of Okhotsk. At some times of the year, such as the month of June, conditions across the western Pacific range from near-subtropical conditions in the south to near-Arctic conditions in the north where ice can still exist in parts of the Sea of Okhotsk (Tyurnin, 1973). It follows that a distinct climate shift (such as an increase in sea surface temperature) might be felt broadly by all eastern Pacific herring, whereas in the western Pacific, populations are already adapted to respond to substantial intra- and inter-annual temperature variation.

We wonder if distributional responses to climate variation have already happened to some putative herring populations. For instance, in the 1950s small herring populations were reported to occur off San Diego, California, in the extreme southern part of the range of Pacific herring (Miller and Schmidtke, 1956), but their present status is uncertain. Spratt, (1981, Table 1) shows records of small (<100 t) catches made regularly in San Diego and Santa Barbara between the early 1920s and early 1950s. Thereafter catch records virtually stopped in 1953 in San Diego and 1961 in Santa Barbara. There are no recent reports that describe the catches or incidental occurrence of herring in the extreme south-eastern Pacific region of California. It seems probable that herring are no

longer permanent residents in these areas and we wonder if such herring populations are extirpated or were they merely episodic, irregular itinerants? The same question might apply to the Yellow Sea herring that seem to appear episodically about every 30 years (Tang, 1981; Hay et al., 2001).

Can the lack of recovery of the Hokkaido-Sakhalin herring be attributed to climate factors? The answer is that we do not know, and we do not have enough definitive information to either confirm or exclude this possibility. It would be irresponsible, however, to complete this brief review without pointing out that this once-mighty stock, one of the largest and longest-fished in the world, is now gone, except for remnants in small isolated areas (Nagasawa, 2001). Noteworthy is that this population was close to the southern edge of its range. Overfishing is implicated in its demise (Hay et al., 2001) but there has now been ample time for recovery – so we end this review with some vexing questions that might be justified from the results we present here. Are herring populations expiring in the southern parts of their range? Is the disappearance of the Hokkaido-Sakhalin population a consequence of climate change in the north Pacific that started many decades ago?

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References

- Atkinson, D., Sibly, R.M., 1997. Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends Ecol. Evol.* 12, 235–239.
- Barton, L., Weststad, V., 1980. Distribution, biology and stock assessment of western Alaska's herring stocks. In: *Proceedings Alaska Herring Symposium*. University of Alaska Sea Grant Report 4, pp. 27–53.
- Blaxter, J.H.S., 1985. The herring: a successful species? *Can. J. Fish. Aquat. Sci.* 42 (Suppl. 1), 21–31.
- Blaxter, J.S.H., Hunter, J.R., 1982. The biology of the clupeoid fishes. *Adv. Marine Biol.* 20, 1–223.
- Carlson, H.R., 1980. Seasonal distribution and environment of Pacific herring near Auke bay, Lynn Canal, southeastern Alaska. *Trans. Am. Fish. Soc.* 109, 71–78.
- Cushing, D.H., 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Adv. Marine Biol.* 26, 249–293.
- Funk, F., 2001. Abundance, biology and historical trends of Pacific herring, *Clupea pallasii*. In: *Alaskan waters*. PICES Scientific Report 17, pp. 86–92.
- Grant, W.S., Utter, F.M., 1984. Biochemical population genetics of Pacific herring (*Clupea pallasii*). *Can. J. Fish. Aquat. Sci.* 41, 856–864.
- Gustafson, R.G., Drake, J., Ford, M.J., Myers, J.M., Holmes, E.E., Waples, R.S., 2006. Status review of Cherry Point Pacific herring (*Clupea pallasii*) and updated status review of the Georgia Basin Pacific herring distinct population segment under the Endangered Species Act. U.S. Department Commercial NOAA Tech. Memo. NMFS-NWFSC-76, 182 p.
- Haeghe, C.W., Schweigert, J.F., 1985. Distribution and characteristics of herring spawning grounds and description of spawning behaviour. *Can. J. Fish. Aquat. Sci.* 42 (Suppl. 1), 39–55.
- Harrison, P.J., Boyd, P.W., Varela, D.E., Takeda, S., Shiimoto, A., Odate, T., 1999. Comparison of factors controlling phytoplankton productivity in the NE and NW subarctic Pacific gyres. *Prog. Oceanogr.* 43, 205–234.
- Hart, J.L., 1973. Pacific fishes of Canada. *Bull. Fish. Res. Bd. Canada* 180, 740 p.
- Hay, D.E., 1985. Reproductive biology of Pacific herring (*Clupea harengus pallasii*). *Can. J. Fish. Aquat. Sci.* 42 (Suppl. 1), 111–126.
- Hay, D.E., McCarter, P.B., 1997a. Larval distribution, abundance, and stock structure of British Columbia herring. *J. Fish Biol.* 51, 155–175.
- Hay, D.E., McCarter, P.B., 1997b. Continental shelf area, distribution, abundance and habitat of herring in the North Pacific. *Wakefield Fisheries Symposium*. Alaska Sea Grant College Program 97-01, pp. 559–572.
- Hay, D.E., McCarter, P.B., Kronlund, R., Roy, C., 1989. Spawning areas of British Columbia herring. A review, geographical analysis and classification, vol. I–VI. *Can. Manuscr. Rep. Fish. Aquat. Sci.* 2019, 1140 p.
- Hay, D.E., Stephenson, R., Toresen, R., Sjöstrand, B., Parmanne, R., Funk, F., Schweigert, J., Tanasichuk, R., Naumenko, N., Radchenko, V., Kobayashi, T., Melvin, G., Power, G., Stevenson, D., Wheeler, J., Claytor, R., Macquinn, I., Jacobsen, J., Malloy, J., Stevenson, K., Watters, D.L., Oda, K.T., Tang, Q., 2001. Taking Stock: an inventory and review of world herring stocks in 2000. An inventory of the world herring populations. In: *Herring 2000: expectations for a new millennium*. University of Alaska Sea Grant, AK-SG-01-04, Fairbanks. pp. 381–454.
- Jørstad, K.E., 2004. Evidence for two highly differentiated herring groups at Goose Bank in the Barents Sea and the genetic relationship to Pacific herring, *Clupea pallasii*. *Environ. Biol. Fishes* 69, 211–221.
- Lindsey, C.C., 1966. Body sizes of poikilotherm vertebrates at different latitudes. *Evolution* 20, 456–465.
- Mackas, D.L., Tsuda, A., 1999. Mesozooplankton in the eastern and western subarctic Pacific: community structure, seasonal life histories, and interannual variability. *Prog. Oceanogr.* 4, 335–363.
- Megrey, B.A., Rose, K.A., Ito, S., Hay, D.E., Werner, F.E., Yamanaka, Y., Aita, M.N., 2007. North Pacific basin-scale differences in lower and higher trophic level marine ecosystem responses to climate impacts using a nutrient-phytoplankton-zooplankton model coupled to a fish bioenergetics model. *Ecol. Modell.*, 196–210.
- Mertz, G., Myers, R.A., 1994. Match/mismatch predictions of spawning duration versus recruitment variability. *Fish. Oceanogr.* 3, 236–244.
- Miller, D.J., Schmidtke, J., 1956. Report on the distribution and abundance of Pacific herring (*Clupea pallasii*) along the coast of Central and Southern California. *California Fish Game* 42, 163–187.
- Myers, R.A., 2001. Stock and recruitment: generalizations about maximum reproductive rate, density dependence, and variability using meta-analytic approaches. *ICES J. Marine Sci.* 58, 937–951.
- Nagasawa, K., 2001. Long-term variations of Pacific herring (*Clupea pallasii*) in Hokkaido and Sakhalin related to changes in environmental conditions. *Prog. Oceanogr.* 49, 551–564.
- PICES, 2001. Report of the 2001 REX workshop on temporal variations in size-at-age for fish species in coastal areas around the Pacific Rim. PICES Scientific Report 20, pp. 1–71.
- Ricker, W.E., 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Bd. Canada* 191, 382 p.
- Rose, K.A., Cowan, J.H., Winemiller, K.O., Myers, R.A., Hilborn, R., 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish. Fish.* 2, 293–327.
- Rose, K.A., Megrey, B.A., Hay, D., Werner, F., Schweigert, J., 2008. Climate regime effects on Pacific herring growth using coupled nutrient-phytoplankton-zooplankton and bioenergetics models. *Trans. Am. Fish. Soc.* 137, 278–297.
- Schweigert, J., Haist, V., 2007. Stock assessment for British Columbia herring in 2006 and forecasts of the potential catch in 2007. Canadian Science Advisory Secretariat Research Document 2007-002, 71 p.
- Shuter, B.J., 1990. Population-level indicators of stress. *Amer. Fish. Soc. Symp.* 8, 145–166.
- Spratt, J.D., 1981. Status of The Pacific Herring, *Clupea harengus peereie*. California Department of Fish and Game Fish Bulletin 171, 107.
- Stout, H.A., Gustafson, R.G., Lenarz, W.H., McCain, B.B., VanDoornik, D.M., Builder, T.L., Methot, R.D., 2001. Status review of Pacific Herring in Puget Sound, Washington. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-45, 175 p.
- Tang, Q., 1981. A preliminary study on the cause of fluctuation in year class size of Pacific herring in the Yellow Sea. *Trans. Oceanol. Limnol.* 2, 37–45. In Chinese with English abstract.
- Taylor, F.C.H., 1964. Life history and present status of British Columbia herring stocks. *Bull. Fish. Res. Board Can.* 143, 81.
- Thompson, W.F., 1916. A contribution to the life-history of the Pacific herring: its bearing on the condition and future of the fishery. Report of the British Columbia Commissioner of Fisheries, pp. 39–87.
- Tyurnin, V.B., 1973. The spawning range of Okhotsk herring. *Izv. Pac. Inst. Fish. Oceanogr.* 86, pp. 12–21 (Translated by Translation Bureau, Department of Secretary of State, Canada).