A review of factors limiting recovery of Pacific herring stocks in Canada

Jacob F. Schweigert, Jennifer L. Boldt, Linnea Flostrand, and Jaclyn S. Cleary

On the west coast of Canada, Pacific herring (*Clupea pallasi*) supported an intensive reduction fishery from the early 1930s until the collapse of all five major stocks in the late 1960s, which then recovered rapidly following a fishery closure. Despite conservative harvests, abundance has declined again recently, with little evidence of recovery. We investigated the effect of bottom-up forcing by zooplankton abundance, top-down forcing by fish and mammal predators, and the effects of sardine abundance as potential competitors on the natural mortality of the herring stock on the west coast of Vancouver Island. Herring mortality was positively related to *Thysanoessa spinifera* and southern chaetognaths and negatively to pteropod abundance. Estimated predation on herring decreased significantly during the years 1973–2008, with the main consumers changing from fish to mammals. However, the correlation with herring mortality was negative, whereas there was a significant positive relationship with sardine abundance. Population recovery is expected to be facilitated by a combination of factors, including adequate food supply, limited or reduced predation (including fishing), and limited competition particularly for wasp–waist systems, where different forage species may occupy similar niches.

Keywords: bottom-up, collapse, competition, Pacific herring, recovery, top-down.

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Introduction

The Thompson–Burkenroad debate about the importance of fishing vs. environment in regulating population abundance underscored fisheries management philosophy early in the past century (Skud, 1975). As longer dataseries have accrued, theories relating population regulation to fisheries management have shifted from single species to multispecies and ecosystem considerations. Consequently, the factors identified as regulators of population decline and recovery have ranged from fisheries and predation in some systems (Bax, 1998; Heath, 2005; Overholz and Link, 2007) to food availability in others (Ware and Thomson, 2005; Frederiksen et al., 2006), climate forcing (Aebischer et al., 1990), or more complex ecosystem interactions (Verheye and Richardson, 1998; Cury et al., 2000; Worm and Myers, 2003; Frank et al., 2005; Mueter et al., 2006). In fact, the relative importance of predation (top-down) vs. food supply (bottom-up) in regulating ecosystems may be a function of the latitude and the complexity of the system (Frank et al., 2007). The ability of a population to recover from overexploitation will depend on the complex interplay of a number of factors in the specific ecosystem.

Pacific herring (*Clupea pallasi*) in British Columbia (BC) are the dominant forage species in the local ecosystem. They have been exploited for at least the past century and have exhibited marked fluctuations in abundance, with periods of depletion in the 1930s and 1960s followed by rapid recoveries (Ware, 1991). The species is relatively short-lived (generally less than 10 years) and matures sexually at age 3, so total abundance is determined largely by annual recruitment. Recruitment in turn is determined by survival during the early life history (Taylor, 1964; Schweigert et al., 2009a).

Since 1986, herring have been managed using a 20% harvest rate in combination with a biomass limit reference point (BLRP) to close the fisheries during periods of reduced abundance. Since these precautionary harvest policies have been in place, all five major populations (Figure 1) have again experienced a marked decline during the past decade (Figure 2a) and at least three have dropped below the BLRP with no signs of recovery, despite annual fishing closures (Schweigert et al., 2009b). Consequently, it appears that ecosystem forcing, such as food supply (bottom-up), predation (top-down), or competition, rather than fishing, could be limiting the recovery of these populations. Herring populations throughout BC have displayed a long-term decline in size-at-age, suggesting that food supply may also have been reduced over the past two decades. In addition, there have been few years of strong recruitment during this period, whereas increased natural mortality rates suggest that predation pressure may also have increased (Figure 2b; Schweigert et al., 2009b). Indeed, the estimated natural mortality rates have been consistently higher than the estimated fishing mortality rates.

Pacific sardine (*Sardinops sagax*) was the dominant forage species in the California Current ecosystem during the first half of the 20th century, but disappeared almost completely by the late 1950s, because of overfishing and adverse environmental conditions (Schweigert, 1988). In the early 1980s, the coast-wide sardine population began to rebuild exponentially off California
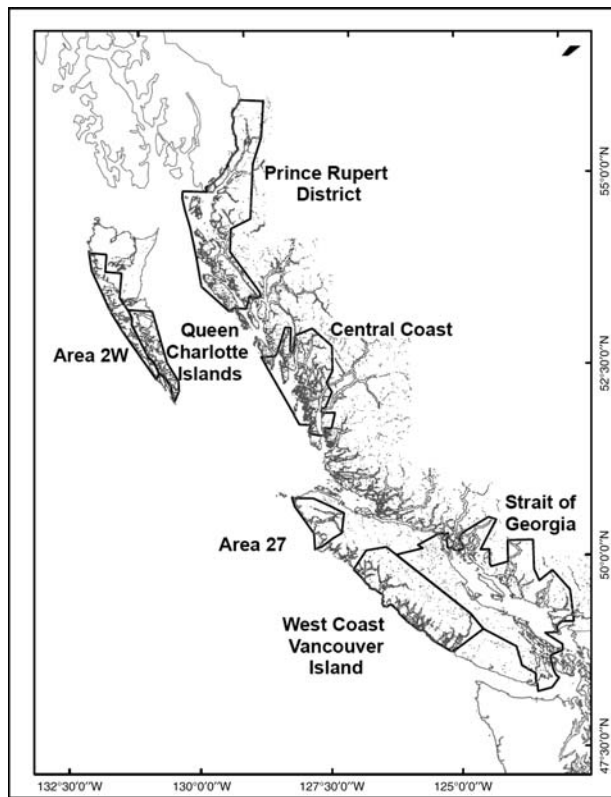
Figure 1. Boundaries of the five major (Queen Charlotte Islands, Prince Rupert District, Central Coast, Strait of Georgia, and west coast of Vancouver Island) and two minor (areas 2W and 27) Pacific herring stocks on the west coast of Canada.

and shortly thereafter resumed annual migrations into Canadian waters (McFarlane and Beamish, 2001). By the late 1990s, the spawning population was estimated to exceed 1 million tonnes and a substantial component of the stock migrated onto the feeding grounds off Vancouver Island (Schweigert et al., 2009c). McFarlane et al. (2005) showed that sardine are opportunistic feeders, consuming a variety of zooplankton and potentially competing for food with herring.

During the past few decades, many marine mammal species that had been substantially reduced in abundance by exploitation (Olesiuk, 2008a, b; Ford et al., 2009) started to recover. Conversely, many predatory fish populations were in decline because of overfishing. Trends in the abundance of food organisms are less clear, with some species of zooplankton increasing, whereas others declined.

Our objective was to examine forcing factors that could facilitate or limit stock recovery of Pacific herring. Indicators of food supply (zooplankton abundance), predation pressure (consumption), and competition (sardine abundance) were compared with the estimates of natural mortality. We focused the analyses on the west coast of Vancouver Island (WCVI) stock, because it has the most complete dataset for ecosystem drivers, but the findings may be relevant to all eastern Pacific populations.

Methods

Natural mortality

For stock assessment and management, five major and two minor migratory populations are recognized, but our analysis focuses only on the WCVI (Figure 1). Annual estimates of adult herring

natural and fishing mortality (Figure 2b) are available from a catch-at-age assessment model that is fitted within a Bayesian estimation framework to time-series data of commercial catch, a spawn index for egg deposition from surveys, and proportions-at-age data (Schweigert et al., 2009b).

Food supply

Synoptic surveys of zooplankton abundance in both inshore and offshore waters off Vancouver Island have been conducted since 1979 (Mackas et al., 2001, 2004). Samples were collected with vertically integrated net tows during four or five seasonally spaced surveys, and nearly all tows used black bongo nets (0.25 m² mouth area) fitted with a TSK flowmeter and 0.23 mm black nylon mesh. Tows were made both day and night to maximize ship utilization. Because capture efficiency of euphausiids may differ between day and night as a consequence of visual avoidance of the net, a correction factor was developed, but this had only limited effects on the results. Subsamples from each tow were counted to species and developmental stage. Abundance (number per m²) was derived from raw counts using subsample fraction, volume filtered, and tow depth. Subsample fraction was varied to give approximately uniform numbers counted (30–50) within each major taxon. Local abundance was converted to dry weight biomass estimates before summing developmental stages within each species. Averages by sampling period were referenced against the long-term seasonal norms to produce log-scale cruise-by-cruise anomalies. Finally, time-series of annual anomalies for each species were calculated by averaging the anomalies from all cruises by year. Statistical aspects of the data are detailed in Mackas et al. (2001), but it should be noted that the anomalies are on a log_{10} scale, making them multiplicative rather than additive.

Data were first summarized by shelf vs. offshore areas and for subareas within the shelf region. However, because the annual anomalies calculated by region followed essentially the same pattern, we used the composite data from all sampling sites as an indicator of food availability in subsequent analyses. Annual anomalies from the baseline average abundance are presented for eight species (groups): boreal shelf copepods (*Calanus marshallae, Pseudocalanus mimus, Acartia longiremis*); Subarctic (oceanic) copepods (*Neocalanus plumchrus, N. cristatus, Eucalanus bungii, Metridia pacifica*); southern copepods (*Paracalanus parvus, Mesocalanus tenuicornis, Clausocalanus* spp., *Ctenocalanus vanus*); northern chaetognaths (*Sagitta elegans, Eukrohnia hamata*); southern chaetognaths (*Sagitta scrippsae*); pteropods (*Limacina helicina*), and two euphausiids (*Euphausia pacifica* and *Thysanoessa spinifera*).

Predation

Marine mammals

Marine mammals that utilize the WCVI and consume Pacific herring in some proportion include primarily part-time visitors (humpback whales—*Megaptera novaeangliae*; northern fur seals—*Callorhinus ursinus*; and California sea lions—*Zalophus californianus*) and year-round residents (harbour seals—*Phoca vitulina*; and Steller sea lions—*Eumetopias jubatus*). Consumption of herring by marine mammals was estimated using methods in Overholz and Link (2007) and Boulva and McLaren (1979). The amount consumed annually depends on mammal abundance, residence time, diet composition, daily ration, weight, age, sex, and temporal and spatial overlap with
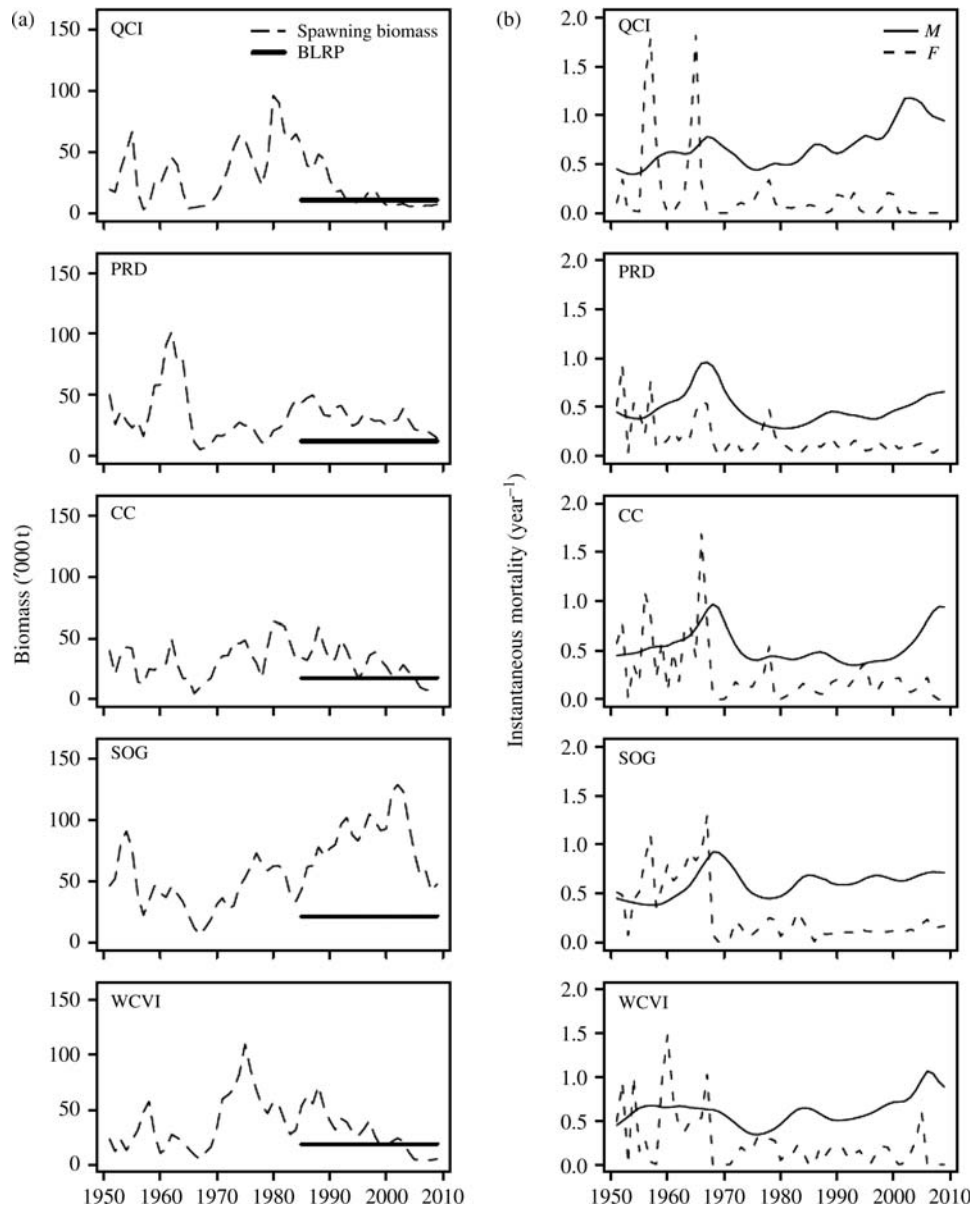
Figure 2. Fluctuations in the five major Pacific herring populations, 1951–2009: (a) abundance and (b) fishing (*F*) and natural (*M*) mortality. QCI, Queen Charlotte Islands; PRD, Prince Rupert District; CC, central coast; SOG, Strait of Georgia; WCVI, west coast of Vancouver Island.

herring. Available information regarding these factors was incorporated where possible (Table 1).

Humpback whales migrate during spring and autumn through BC waters, where they forage on zooplankton, particularly euphausiids, and forage fish, such as Pacific herring (Ford *et al.*, 2009). Witteveen *et al.* (2006) suggested that humpback whales consume fish in proportion to their availability in the water column (as sampled with a midwater trawl), where they are actively feeding. Ware and McFarlane (1995) estimated that herring comprised approximately 17% of the pelagic fish species in the La Perouse Bank area (off southwest Vancouver Island) during the 1980s. Because diet data are not available for humpback whales on the WCVI, 17% of their diet was assumed to be herring.

Northern fur seals are migratory and approximately one-third of the North Pacific population winters off the coast of North

America (DFO, 2007). Approximately one-third of this group resides for an estimated 3.1 months (~91 d) in coastal BC waters (Olesiuk, 2008a) at some point during December–May (DFO, 2007). Females comprise the majority of animals that winter in the La Perouse Bank area foraging on herring (DFO, 2007). Adult and subadult male California sea lions also winter in BC waters (~240 d; Hancock, 1970; Bigg, 1985).

Harbour seals are year-round residents of coastal BC waters (Baird, 2001). Because seasonal variations in their diet on the WCVI are poorly known, we assumed that herring are available to harbour seals in nearshore waters throughout the year and that the diet of harbour seals sampled southwest of Vancouver Island during July–October (1988/1989) is representative (Olesiuk *et al.*, 1990). Steller sea lions are also year-round BC residents, but breeding animals do not forage during the 1–3 months

Table 1. Methods and sources of information utilized in estimating the consumption of herring by marine fish and mammal predators (n.a., not applicable; BC, British Columbia; DFO, Department of Fisheries and Oceans; INPFC, International North Pacific Fisheries Commission; IPHC, International Pacific Halibut Commission; NMFS, National Marine Fisheries Service; WCVI, west coast of Vancouver Island; C, annual consumption; B, biomass; A, abundance; m, body mass; R, daily ration; P, proportion of herring; D, number of days).

Species	C method	B (in t) or A source	m (g), P, and/or R	D
Hake	See text, Elliot and Persson (1978), and Worobec (1984)	Linearly interpolated acoustic and bottom-trawl survey B estimates, 1977–2007. Assumed: $B_{1973-1976} = B_{1977}$; $B_{2008} = B_{2007}$. See text	m = n.a.; $P = 0.0011$ (Tanasichuk et al., 1991)	138
Sablefish	Ware and McFarlane (1986): $C = BP8.2m^{-0.26}$	Assumed: $B_{1973-1992} = 18\,000$ (Ware and McFarlane, 1986); $B_{2007,2008} = B_{2006}$; 20% of exploitable BC stock (Cox et al., 2009) off WCVI (Ware and McFarlane, 1986)	$m = 2\,236$; $P = 0.06$ (Ware and McFarlane, 1986)	n.a.
Pacific cod	As above	$B_{1973-2002}$ from Starr et al. (2002); assumed: $B_{2003-2008}$ = average B during previous 10 years	$m = 1\,994$; $P = 0.39$ (Ware and McFarlane, 1986)	n.a.
Spiny dogfish	As above	$B_{1980-2001}$ from NMFS triennial survey in Vancouver INPFC area north of 47.5°N (J. King and M. Wilkins, pers. comm.); $B_{2002-2008}$ from DFO triennial groundfish trawl survey (R. Stanley, pers. comm.). Interpolated between survey years; no correction for catchability	$m = 1\,594$ (R. Tanasichuk, pers. comm.); $P = 0.15$ (Tanasichuk et al., 1991)	n.a.
Arrowtooth flounder	As above	As above	$m = 2\,755$ (Turnock and Wilderbuer, 2009); $P = 0.13$ (Pearsall and Fargo, 2007)	n.a.
Lingcod	As above	$B_{1977-1996}$ from Leaman and McFarlane (1997); assumed: $B_{1997-2008}$ = average B	$m = 2\,250$ (Fargo et al., 1988); $P = 0.88$ (Pearsall and Fargo, 2007)	n.a.
Pacific halibut	As above	$B_{age\,6+}$ assuming 25% of biomass in IPHC area 2B occupied the area off WCVI (S. Hare, pers. comm.); assumed: $B_{2008} = B_{2007}$	$m_{1997-2008}$ (Hare and Clark, 2008); $m_{1973-1996}$ = average $m_{1997-2003}$ (11 188 g); $P = 0.39$ (Ware and McFarlane, 1986)	n.a.
Humpback whales	Overholz and Link (2007): $C = APD\omega(m/1000)^{\tau}$, where $\omega = 0.123$ and $\tau = 0.80$ (Innes et al., 1987)	$A_{1992-2005}$: 20% (approximate % of sightings on WCVI) of reduced-bias abundance estimate; assumed: 4.1% population growth rate during 2006–2008 (Ford et al., 2009)	$m = 34\,000\,000$ (Ford et al., 2009); $P = 0.17$ (average in La Perouse pelagic fish sampled during 1980s; Ware and McFarlane, 1995)	184
Northern fur seals	As above	To estimate female $A_{1973-2008}$, ratio of A_{2006} females in BC (=123 750; DFO, 2007) to number of pups born on Pribilof Islands in 2006 (~132 000) applied (Fritz, 2007)	$m = 35\,000$ (females only; DFO, 2007); $P = 0.45$ (Olesiuk, 2008a)	91 (Olesiuk, 2008a)
California sea lions	As above	A interpolated between estimates from Bigg (1985) and Olesiuk (2008b)	$m = 300\,000$ (males only); $P = 0.35$ (http://www.racerocks.com/racerock/rreo/rreoref/mmammals/sealsandsealions.htm)	240
Steller sea lions	$C = ADPR_{males} + ADPR_{females}$	$A_{2006} = 24\,000$ in BC (DFO, 2008); assumed: 3.5% population growth rate (Olesiuk, 2008a). To estimate number off WCVI, ratio "summer non-pup counts off WCVI"/"total BC counts" applied (Olesiuk, 2008b)	$P = 0.25$ (Womble and Sigler, 2006; Trites et al., 2007). $r = 32.5$ kg food d^{-1} (males) or 17.5 kg food d^{-1} (females; DFO, 2008)	304
Harbour seals	Boulva and McLaren (1979): $C = APD\omega(m_{males}/1000)^{\tau} + APD\omega(m_{females}/1000)^{\tau}$, where $\omega = 0.089$ and $\tau = 0.76$	A_{1976} from Olesiuk (1999); assumed: 17.2% population growth rate for other years	$m = 83\,000$ males age 10; $m = 66\,000$ females age 14 (Olesiuk, 1993); assumed diet on WCVI = diet in Strait of Georgia; $P = 0.324$ (Olesiuk et al., 1990)	184

they spend on rookeries, whereas non-breeding animals forage year-round (Olesiuk, 2008b). We assumed that all animals might consume herring during 10 months of the year (304 d).

Fish

Groundfish constitute a large proportion of the biomass in marine waters off the WCVI. Species consuming herring as a portion of their diet include Pacific hake (*Merluccius productus*), sablefish (*Anoplopoma fimbria*), arrowtooth flounder (*Atheresthes stomias*), Pacific halibut (*Hippoglossus stenolepis*), Pacific cod (*Gadus macrocephalus*), spiny dogfish (*Squalus acanthias*), and lingcod (*Ophiodon elongates*). In addition, Chinook salmon (*Oncorhynchus tshawytscha*) feed on herring. Information on methods and data sources is summarized in Table 1.

Because there is more information available on Pacific hake than for the other species, a more elaborate approach was used to estimate their consumption of herring. There are both migratory and resident Pacific hake stocks in BC, but the latter are considerably less abundant and they were therefore excluded from the analysis. Migratory hake generally enter BC waters in mid-June and leave in October (~138 d; Beamish and McFarlane, 1985). Acoustic and bottom-trawl estimates of hake biomass in the International North Pacific Fisheries Commission's Vancouver region were acquired for 1977, 1980, 1983, 1986, and 1989 (Dorn *et al.*, 1994). Because the acoustic surveys only covered the southern WCVI portion of BC, the information derived from these represent minimum biomass estimates. More recently, transect-specific integrated acoustic (using a different target strength) and trawl-survey estimates off Vancouver Island have become available for 1992, 1995, 1997, 1999, 2001, 2003, 2005, and 2007. Although not ideal, biomass estimates from the periods before and after 1992 were combined and linearly interpolated between survey years to construct a time-series for 1977–2007. Biomass in 2008 was assumed equal to 2007 and that in 1973–1976 equal to 1977. However, only a small proportion of the hake population is large enough to consume herring. Annual estimates of the piscivorous fraction during 1991–2005 were multiplied by the biomass estimates in each year, and an average piscivorous proportion (0.056) was used for all other years.

The daily consumption rate of hake was estimated for each year and month as a function of evacuation rate and the average amount of herring found in the stomachs, using methods similar to Rooper and Haldorson (2000) and the Elliot and Persson (1978) model. The average amount of herring in hake stomachs was assumed constant during daylight (11% of body weight; Tanasichuk *et al.*, 1991). The evacuation rate (h^{-1}) was estimated using the Worobec (1984) model, based on average monthly sea surface temperatures at Amphitrite Point (http://www-sci.pac .dfo-mpo.gc.ca/osap/data/lighthouse/amphitrt.txt, last accessed 18 September 2009). Average monthly daylight hours were estimated for an equivalent latitude (48.92°N; http://astro.unl.edu/ classaction/animations/coordsmotion/daylighthoursexplorer .html, last accessed 14 October 2009). Total consumption of herring was then estimated by multiplying the daily consumption by hake biomass and the number of days in each month, then summed over all months in each year.

For other groundfish species, the annual consumption was estimated as a function of predator biomass, mean body mass, and the proportion of herring in the diet (Ware and McFarlane, 1986). Biomass estimates for each species were taken from a variety of

sources, and some assumptions, interpolations, or extrapolations were necessary to acquire complete time-series (Table 1).

Chinook salmon is a migratory species, with many stocks occupying the area off the WCVI during part of the year (Trudel *et al.*, 2009). Annual abundance was based on the estimated number that was vulnerable to the local troll fishery off the WCVI. Following the methods of Robinson (2000), annual consumption of herring was estimated as a function of biomass (abundance multiplied by average body mass), daily ration, and number of days residence, but the amount eaten was negligible compared with the other predators.

Competition

We used the annual coast-wide sardine spawning-biomass estimates from the stock assessment by Hill *et al.* (2009) as an index of the competitor biomass contributing to herring natural mortality.

Models

A suite of generalized linear models was developed using the R statistical package to link estimated Pacific herring natural mortality to the zooplankton indices, fish and marine mammal predation estimates, and sardine abundance for the period 1985–2008 where data were available for all variables. The step-AIC function from the MASS library was used to derive the best model. Linear models and loess smoothers were also fitted to the entire time-series of data to illustrate the relationships between individual forcing factors and herring natural mortality rate.

Results

The boreal shelf copepods displayed a general downward trend in abundance over the time-series, whereas the Subarctic copepods experienced a decline through the early 1990s and have subsequently increased (Figure 3). The southern copepods fluctuated in abundance more or less in conjunction with strong El Niño events (1982/1983, 1992/1993, 1997/1998, and 2002/2003) and resultant periods of warmer and colder water off WCVI. Subarctic copepods, *E. pacifica* and *T. spinifera*, displayed an increasing trend in abundance as did the southern chaetognaths. Northern chaetognaths and pteropods declined over the timeseries. Fits of linear models to zooplankton anomaly data and herring natural mortality rate for 1979–2008 (Figure 4) indicated significant positive relationships for *T. spinifera* ($r^2 = 0.24$, $p < 0.01$), and southern chaetognaths ($r^2 = 0.52$, $p < 0.001$), and a significant negative one for pteropods ($r^2 = 0.30$, $p < 0.01$). In addition, the loess smoother suggests positive relationships with the two euphausiid species and negative ones for boreal shelf copepods and northern chaetognaths.

Total annual consumption of Pacific herring by the 13 predators examined ranged from 45 000 t (in 2008) to 87 000 t (in 1988) with an average of 61 000 t consumed annually during 1973–2008 (Figure 5). On average, the primary predators of herring included Steller sea lions, northern fur seals, hake, lingcod, Pacific cod, and spiny dogfish (Table 2 and Figure 5). Total annual consumption decreased over time ($r^2 = 0.47$, $p < 0.001$), because of the decline in consumption by fish predators ($r^2 = 0.38$, $p < 0.001$)—primarily caused by decreasing biomasses after 1992—accompanied by a slight decrease in consumption by marine mammals ($r^2 = 0.19$, $p < 0.01$). Despite the decreasing population of northern fur seals, the increasing populations of Steller sea lions and humpback whales resulted in increased
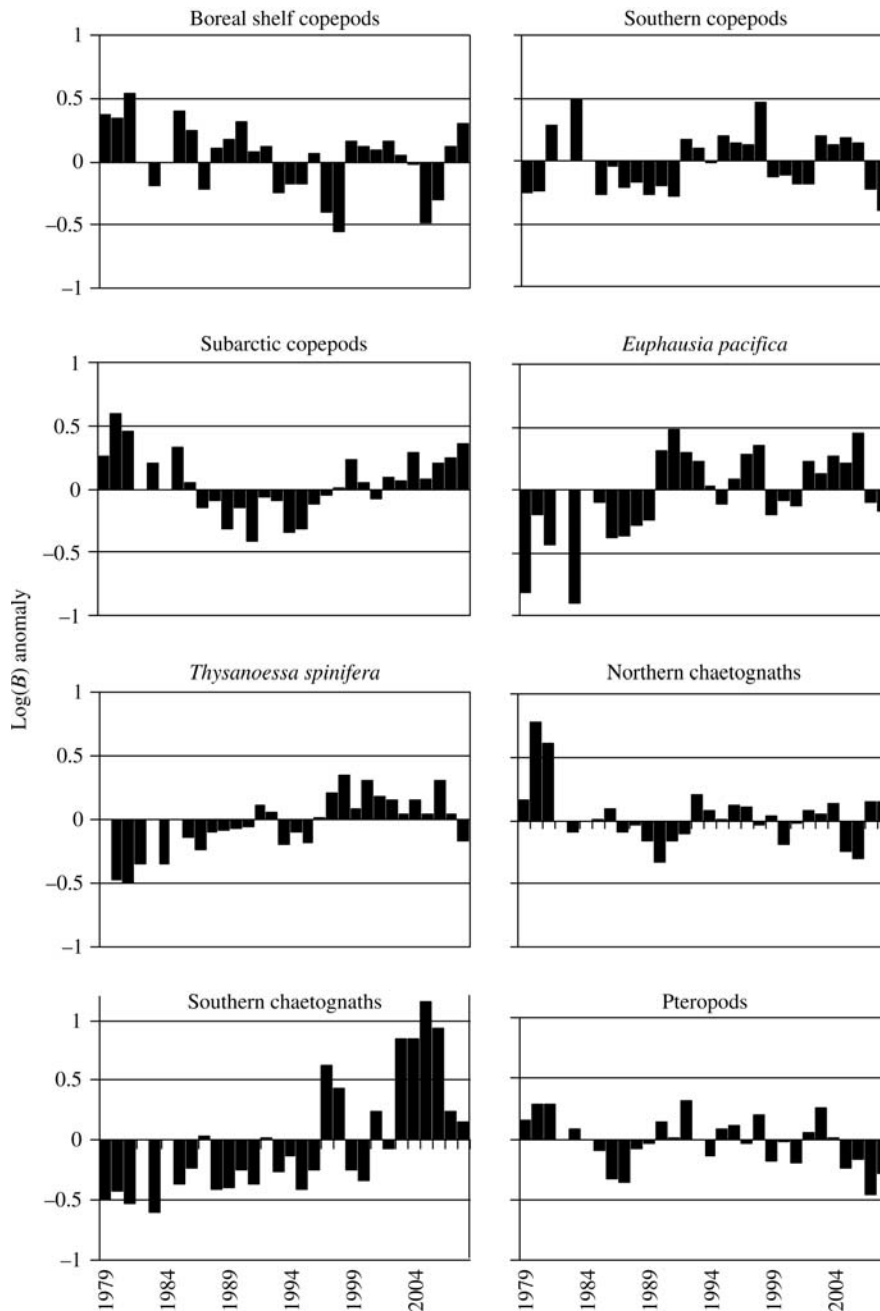
Figure 3. Estimated biomass anomalies for key zooplankton species groups on the WCVI, 1979–2008.

consumption by mammal predators since 1980. The correlation between herring natural mortality and the consumption of herring (Figure 6) was significant and negative for marine mammals ($r^2 = 0.17$, $p = 0.012$), for fish ($r^2 = 0.42$, $p < 0.001$), and for the total ($r^2 = 0.51$, $p < 0.001$). Marine mammal abundances during the 1970s were largely assumed rather than estimated and, when excluded from the correlation, consumption by marine mammals is positively correlated with herring natural mortality ($r^2 = 0.18$, $p < 0.05$). Excluding the 1970s data does not alter the negative relationship between herring natural mortality and total predator consumption or fish predator consumption.

Pacific sardine abundance increased exponentially until 2000, then stabilized at a somewhat lower level (Figure 7). Overall, the

relationship between herring natural mortality and sardine abundance was positive and significant ($r^2 = 0.42$, $p < 0.001$).

Of the suite of models examined through the step-AIC analysis, the model with the lowest AIC value explaining variation in herring natural mortality included Subarctic copepods, southern chaetognaths, pteropods, and Pacific sardine ($r^2 = 0.88$, $p < 0.001$).

Discussion

The factors affecting the recovery or non-recovery of depleted populations in response to management are complex and appear to vary among different systems (Frank *et al.*, 2007). Ware and Thomson (2005), Frederiksen *et al.* (2006), and Perry and Schweigert (2008) presented evidence of bottom-up control of
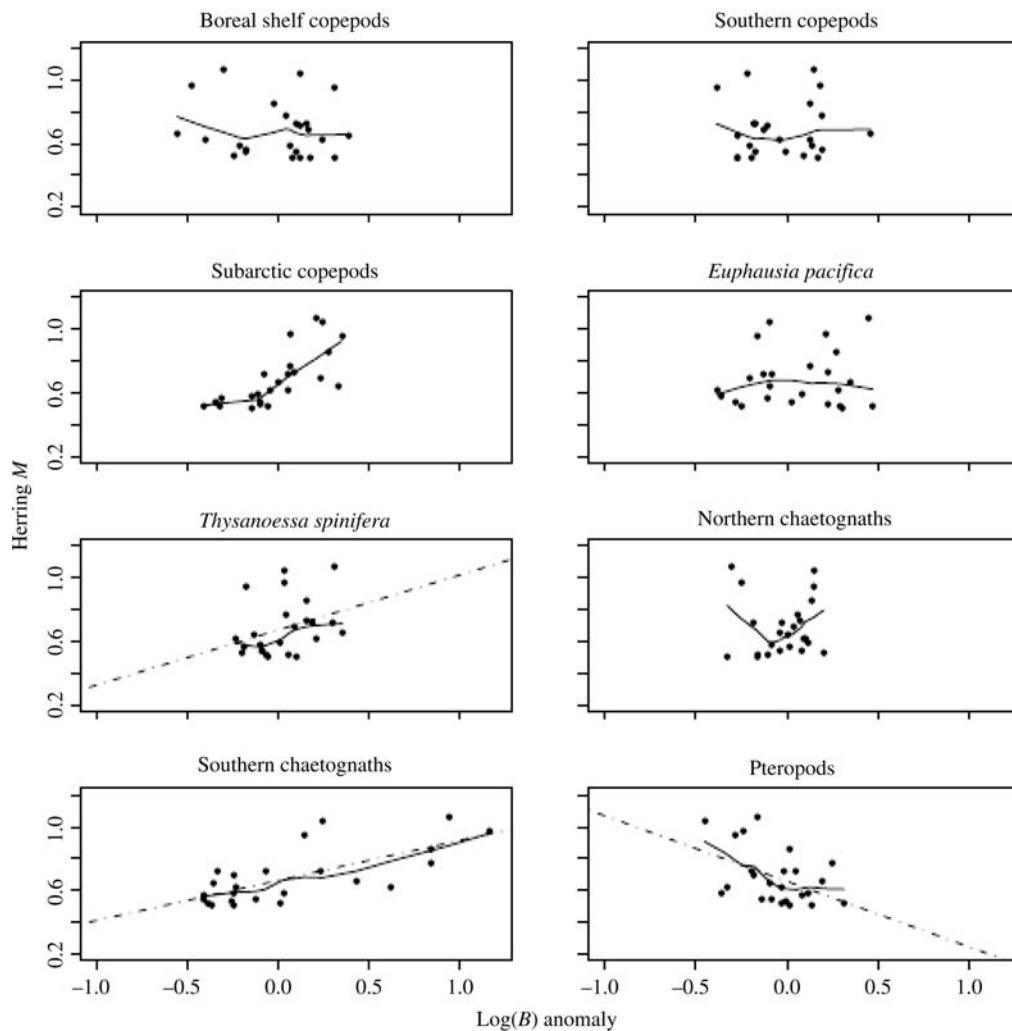
Figure 4. Relationship between herring natural mortality (M) and zooplankton biomass [log(B)] anomalies for key species groups on the WCVI, 1979–2008, with loess smoother (solid) and linear regression if significant (dashed, $p < 0.01$).

production in ecosystems, whereas others provide evidence of top-down control (Bax, 1998; Worm and Myers, 2003). "Wasp–waist" systems dominated by forage species are susceptible to both top-down and bottom-up controls that can be altered by fishing effects (Cury *et al.*, 2000; Frank *et al.*, 2005), even pushing the system into a "predator pit" (Bakun, 2006). A similar effect could be envisioned from closely allied, competing species resulting in a switch in dominance (Skud, 1982), with the subordinate species being relegated to a "competition pit".

The Pacific herring populations off the west coast of Canada have experienced exploitation for more than a century and have gone through at least two collapses and recoveries during that period (Hourston, 1980; Ware, 1991). Ware (1991) reported Tester's (1948) discovery that herring recruitment to the spawning population and subsequent survival are negatively related to sea surface temperature and noted that the periods of reduced herring productivity are associated with warm-water conditions. However, the causal mechanism is not well understood: bottom-up as well as top-down forcing or some other factors, might affect the observed cycles in herring production. Interestingly, the reduced survival of adult herring is most pronounced in the regions exposed to offshore influences (WCVI,

Queen Charlotte Islands, and to a lesser extent Central Coast; Figure 2b), where the effects of competition with sardines should be most pronounced. The Strait of Georgia herring population, which migrates out to the WCVI to feed (Tanasichuk, 2000), has remained above the BLRP. This may be because of the recruitment processes during the first year of life, when these fish remain in the relatively benign waters within the Strait, where they are not affected by competition with sardine.

The significant positive relationships between herring natural mortality and Subarctic copepods and southern chaetognaths and the negative one with pteropod abundance are puzzling, because neither of these groups are recorded as important prey for herring. However, these species may simply be an indicator of the presence of California Current waters that are dominated by less nutrient-rich plankton; therefore, this could result in poorer feeding conditions for adult herring. Although adult herring feed almost exclusively on euphausiids (Wailes, 1936), a significant relationship was only observed with *T. spinifera*. Possibly, the bottom-up effects are mediated through competition for food with Pacific sardine, which may reduce the available food supply, thereby inhibiting population recovery. Herring and sardine share many of the same feeding grounds and exploit
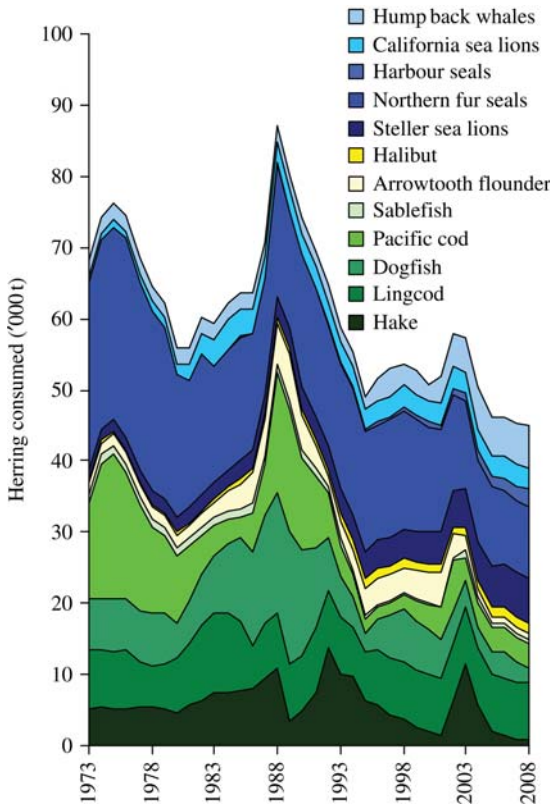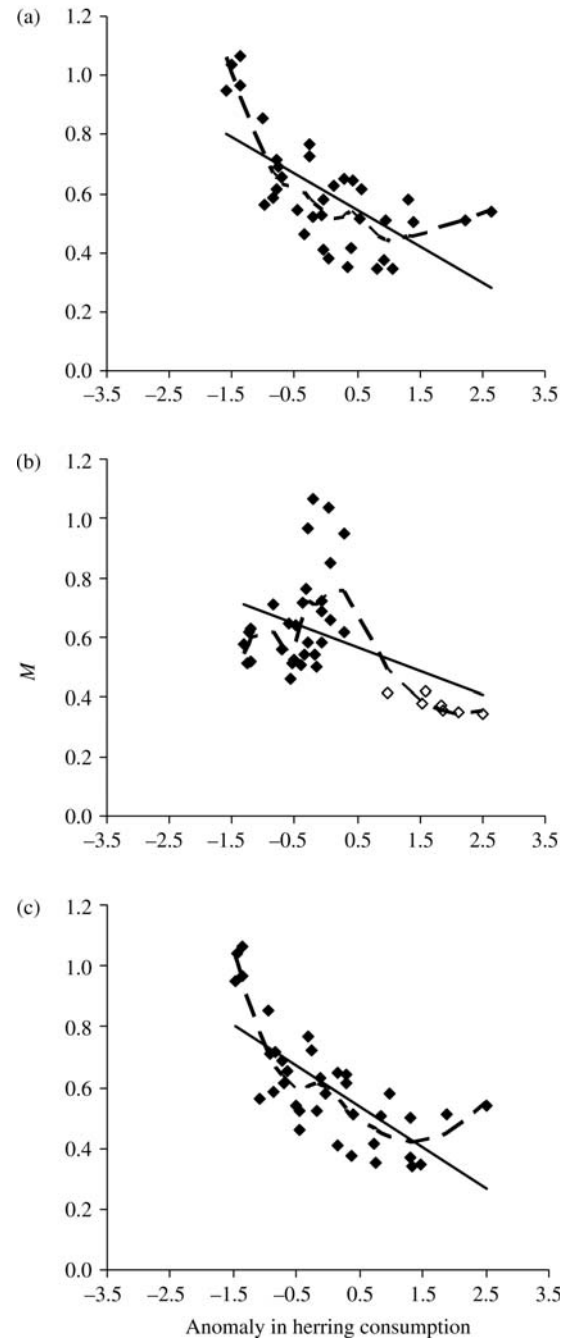
Figure 5. Estimated consumption of herring by the major predator populations on the WCVI, 1973–2008.

Table 2. Estimated average biomass (B), and average consumption of Pacific herring (C), expressed as a percentage of the average Strait of Georgia and WCVI herring SSB (%) for each predator, 1973–2008 (standard errors are in parenthesis).

Species	B (t)	C (t)	Percentage
Humpback whale	13 578 (5)	3 000 (225)	2.6
California sea lion	802 (45)	2 647 (149)	2.3
Harbour seal	181 (42)	458 (106)	0.4
Northern fur seal	7 165 (336)	17 723 (831)	15.7
Steller sea lion	1 781 (130)	3 385 (246)	3.0
Halibut	16 640 (1 187)	887 (64)	0.8
Arrowtooth flounder	20 572 (1 871)	2 773 (252)	2.5
Sablefish	13 283 (961)	880 (64)	0.8
Pacific cod	7 526 (937)	7 526 (937)	6.8
Dogfish	40 958 (3 798)	7 406 (687)	6.7
Lingcod	8 310 (205)	8 060 (199)	7.1
Hake (piscivorous)	11 803 (1 017)	5 818 (508)	5.1
Total			53.8

Figure 6. Relationship between herring natural mortality (M) and the annual anomaly in consumption of herring, 1973–2008, by: (a) fish; (b) marine mammals (open symbols represent data from the 1970s); and (c) all predators combined. Loess smoother (dashed) and linear regressions (solid) are indicated.

some of the same prey (McFarlane *et al.*, 2005), although sardine are filter-feeders.

Another factor affecting the recovery of depleted herring populations might be top-down predation. In estimating consumption of WCVI herring, Ware and McFarlane (1986, 1995) found that three predators (hake, sablefish, and Pacific cod) accounted for the consumption of 29–54% of the adult stock. In the current analysis, fish and marine mammals consumed an average of 60 563 t of herring, which represents up to 54% of the average estimated spawning-stock biomass (SSB) of the combined WCVI and

Strait of Georgia stocks that mix on La Perouse Bank (Table 2). This value may be an overestimate, because the SSB is a minimum estimate and does not include herring younger than 3 years of age. The estimated percentage consumption is within the range estimated by Ware and McFarlane (1986, 1995). Nevertheless, consumption did not appear to be a significant factor affecting the WCVI herring stock. Novel is the indication that the primary predators of herring changed from fish to
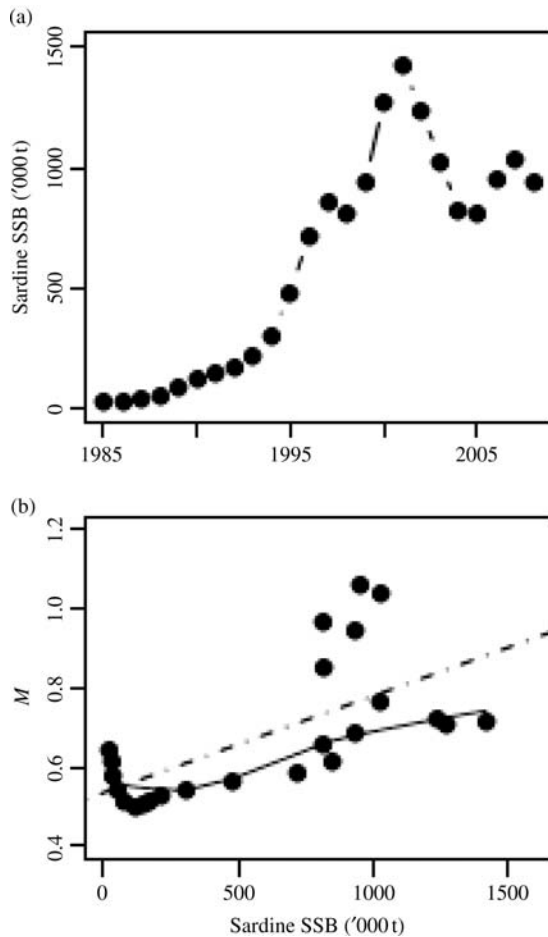
Figure 7. (a) Estimated sardine SSB from Hill *et al.* (2009); and (b) relationship between herring natural mortality (*M*) and sardine SSB with loess smoother (solid) and linear regression (dashed).

marine mammals in 1995, caused by the decrease in fish biomass and the increase in the abundance of some marine mammals.

Assumptions regarding predator diet composition, biomass, and abundances may have biased the estimates of total or relative consumption by different predators. For example, the estimate of northern fur seal consumption may primarily reflect immature herring mortality, because their foraging is concentrated within the 50–200-m isobath during December–May (DFO, 2007), when adult herring are largely restricted to inshore spawning locations. The predator biomass time-series used reflect the best available estimates, but these have often been interpolated or are based on the average values. In addition, some estimates of biomass (e.g. hake for 1973–1991) were based on biomass indices (not total biomass) and represent minimum estimates. The triennial groundfish trawl-survey biomass estimates for spiny dogfish and arrowtooth flounder may also be underestimates. In addition, we did not consider other potential predators, such as coho salmon, rockfish, mackerel, Pacific white-sided dolphins, harbour porpoises, or seabirds, because time-series of abundance and diet composition for these are sparse. Chinook salmon predation was estimated, but it is insignificant compared with the other predators we examined. Nevertheless, although predation was not a significant factor in the model that best explained variation in herring natural mortality, the analyses indicate that a

substantial proportion of the herring population could be cropped annually by predation. Perry and Schweigert (2008) estimated the carrying capacity for herring in this area at roughly 200 000 t, indicating that even under ideal conditions, the predator community could have a significant effect on the prey abundance.

The analysis of top-down effects suggests that there is not a causal relationship between herring natural mortality and consumption by marine mammals or fish, because the negative relationship is opposite to expectations. The trends could therefore simply reflect coincidences in abundance time-series and not necessarily indicate a causal relationship. In addition, we did not address autocorrelation, because several values in the time-series were interpolated or simply assumed. Predator abundance data were less reliable in some cases for the 1970s and indicated high marine mammal consumption associated with low herring natural mortality. When data from this period were eliminated, it resulted in a positive correlation between marine mammal consumption and herring natural mortality rate, but no change in the relationship between herring natural mortality and total predator consumption or fish predator consumption. Similarly, we assumed that herring represented a constant fraction of the diet usually, whereas fluctuations in herring abundance may well influence their vulnerability to predation and their frequency in the diet. Hence, the top-down effects are by no means clear and require further research and better data.

The dynamics of population recovery are likely species- and ecosystem-specific and may depend on the degree of perturbation and the effect of other species on the depleted target species. Understanding the ecosystem interactions depends on the quality and quantity of data available for the various components. Despite the WCVI being the best-studied area of the BC coast, it proved extremely difficult to synthesize the information available on even the major predators. One might expect a dynamic species, such as herring, to recover rapidly from a depleted state, because of their ability to produce large numbers of progeny during favourable periods, thereby effectively swamping their predators. However, successful recovery requires adequate food resources to support growth and a limited predator community. Although managers may limit fishing, controlling food resources and predator abundance is not feasible. In addition, any large-scale changes in the ecosystem may present a stressor on the niche of the target population. In this case, the large increases in Pacific sardine since the early 1990s and their seasonal occupation of the WCVI could have a profound effect on herring as a potential competitor for food, as well as an attractor of predators that may supersede its role as a buffer against predation. Ultimately, the ability of Pacific herring to recover to some extent will be serendipitous, depending on the appropriate coincidence of an abundant food supply, limited competition, and a reduced predator community.

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