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Vertebrate exploitation of pulsed marine prey: a review and the example of spawning herring

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Abstract Short-term bursts of prey availability occur in many ecosystems and have potential important consequences for both predator biology and ecosystem function. Examples of prey 'pulses' in marine ecosystems include spawning runs of several anadromous and marine fishes, horseshoe crab spawning, and salmonid juvenile outmigrations, which are exploited by numerous species of vertebrate predators. In a few cases, the fitness or demographic consequences of such predator–prey interactions are known or inferred, but too often that information remains unknown. We explored the extent of temporal and spatial variation in one example of a pulsed marine resource: the spawning of Pacific herring (*Clupea pallasii*). Spawning herring provide a rich, aggregated resource to which dozens of species of vertebrate predators often exhibit strong numerical responses. However, the spawning events are often variable in both time (annual differences of several to many weeks) and space (both regional and more local differences in size and timing of events). Such variability must affect more mobile predators less than area-restricted predators, and thus its effect would vary not only among species but also within species, depending on constraints of the predator life history. Unpredictability of the prey concentrations, whatever their proximate causes, may contribute to maintenance of metapopulations of prey such as herring, if unpredictability lessens the impact of predation.

Keywords *Clupea pallasii* · Pacific herring · Pulsed resources · Short-term prey exploitation · Vertebrate predators in marine ecosystems

Introduction

The availability of most food resources varies in ecological time (e.g., Odum et al. 1995; Ostfeld and Keesing 2000). Some resources vary on very long time scales, such as the multi-decadal seeding cycles of semelparous bamboos (Janzen 1976). Toward the other end of the frequency spectrum are tidal cycles, predictable on both daily and monthly cycles. Between these two extremes lie

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numerous examples of variation of food resources, of differing duration and predictability. There are many examples of seasonal variation in resource availability and consumer use, with durations commonly measured on a scale of weeks or months: e.g., berries by bears and thrushes (e.g., Thompson and Willson 1979; Willson and Gende 2004), flowers by pollinators (e.g., Paton 1986), caterpillars by birds (e.g., Lack 1966), salmon by bears and eagles (e.g., Gende et al. 2004). In addition, the several-year cycles of some rodents, hares, grouse and their predators are well known (e.g., Newton 1998).

In this paper, we focus on distinctive types of seasonal resources and resource use that occur in ‘‘pulses’’; specifically, we focus on single species of marine prey that are used by vertebrate predators for relatively short periods (days to a few weeks), usually every year. Pulsed resource use is thought to be important to predator biology even though it is short-term and likely to be severely underestimated in annual and off-season tallies of prey consumed (Womble et al. 2005). Pulsed resources have the potential to influence not only predator population dynamics and fitness but also trophic cascades, nutrient cycling, and ecosystem function (Yang 2004). Examples of short-term, regular pulses of prey availability and corresponding bursts of predator exploitation, or short-term bursts of exploitation of more stable prey, can be found in many ecosystems (Odum et al. 1995; Ostfeld and Keesing 2000), but here we emphasize those associated with some marine systems.

The paper is organized in two main sections. The first is a brief review of several cases of short-term predator–prey interactions, high-lighting those for which some fitness or demographic consequences have been inferred. We then present a more detailed survey of one specific example of a pulsed marine prey (spawning herring and their eggs), first reviewing some basics of herring biology and the predators that gather at herring runs, and then exploring the variability of this prey resource. We close by noting some general issues relevant to the issue of pulsed-prey exploitation and emphasizing some research opportunities.

Review of short-term prey use in marine systems

An array of selected examples, chiefly from North America, includes birds, mammals, and fishes as predators, and both invertebrates and fishes as prey (Table 1). These cases typically involve aggregations of numerous predators of one or more species. In the case of whale sharks (*Rhinodon typus*), the absolute numbers of predators may not be so great, but the accumulation of predator biomass is likely to be significant in terms of impact on the prey.

Because few studies have focused on the ecology of short-term prey exploitation, we commonly lack information on the consequences of such consumption for the predators (or the prey). For example, feeding on eulachon (*Thaleichthys pacificus*) runs in spring may be important to Steller sea lion (*Eumetopias jubatus*) breeding success, because adult sea lions need to store energy before fasting at the breeding rookeries (males) and feeding newborn pups (females) (Womble et al. 2005). The possible fitness consequences have yet to be measured for this interaction, but there is evidence that prey availability can affect the reproductive success of pinnipeds (e.g., Soto et al. 2004, 2006; Trillmich and Ono 1991). Similarly, feeding on eulachon runs may help fuel migration for such species as Thayer’s gull (*Larus thayeri*) (Willson et al. 1998), but we have no measures of weight gain or migration success to support this relationship. Feeding on salmon runs probably enhances reproductive success of bears (*Ursus arctos*, *U. americanus*) and may facilitate feeding and survival of juvenile bald eagles (*Haliaeetus leucocephalus*) (Willson et al. 1998), but supporting data are few (Hilderbrand et al. 1999).

In a few cases, however, there are indications that short-term exploitation has consequences for predator biology. The shorebirds that feed heavily on horseshoe crab (*Limulus polyphemus*) eggs in Delaware Bay are long-distant migrants, arriving in lean condition from southern South America and preparing for another long flight to Arctic breeding grounds (Weidensaul 1999). They can almost double their body weight in 2–3 weeks by feeding voraciously on horseshoe crab eggs

Table 1 Selected examples of short-term prey exploitation by vertebrates in marine systems

Prey	Predators	Location	Season	Duration	References
Eulachon spawning runs	Steller sea lions, harbor seals, bald eagles, gull species, others	Northeastern Pacific, lower river reaches and estuaries	Spring	2–3 weeks	Willson et al. (1998), Marston et al. (2002), Sigler et al. (2004), Womble et al. (2005)
Capelin (*Mallotus villosus*) spawning runs	Common murres, Atlantic puffins (*Fratercula arctica*), others	Northwestern Atlantic, beaches	Summer	< 6 weeks?	Pierotti et al. (1988), Piatt (1990)
Pacific herring	See text	North Pacific	Spring	Usually < 2 weeks	See text
Pacific salmon (*Oncorhynchus* spp.) spawning adults	Black and brown bears, wolves (*Canis lupus*), bald eagles, corvids, gull spp., others	North Pacific streams and estuaries; introduced populations in interior systems	Usually summer or fall; sometimes spring	A few weeks in small coastal streams; much longer in some streams	McClelland et al. (1982), Willson and Halupka (1995), Willson et al. (1998), Restani et al. (2000), Dickerson et al. (2002), Gende et al. (2004)
Pink salmon eggs	Coast-range sculpin (*Cottus aleuticus*)	Alaska	Summer	A few weeks	McLarney (1967)
Pink and chum salmon (*O. keta*) outmigration	Herring, charr (*Salvelinus* spp.), Pollock (*Theragra chalcogramma*), juvenile salmon, sculpins (*Cottus* spp.),terns (*Sterna* spp.), northwestern crows, gulls, mergansers	B.C., southeastern Alaska	Spring	1–4 weeks	Wood (1987, Heard (1991); pers. comm., R. H. Armstrong, Juneau AK; MFW personal obs.
Sockeye salmon (*O. nerka*) outmigration	Arctic charr (*Salvelinus alpinus), lake trout (S. namaycush), terns, sculpin, other salmon, others*	Alaska	Late spring to early summer	~ 2 weeks	Burgner (1991), Taylor and Lum (2005)
Salmonid smolts	Mergansers	Norway	June	About 3 weeks	Kålås et al. 1993
Snapper spp. (*Lutjanus cyanopterus* and *L. jocu*) spawn; possibly also jellyfish feeding on spawn	Whale sharks	Caribbean near Belize	Spring	About 2 10-day periods; evenings only	Heyman et al. (2001); pers. comm. W. D. Heyman, The Nature Conservancy, Punta Gorda, Belize; similar response to coral spawn in Western Australia (cited in Heyman et al. (2001))

Table 1 continued

Prey	Predators	Location	Season	Duration	References
Horseshoe crab eggs	Red knots, sanderlings (*C. alba*), semipalmated sandpipers, ruddy turnstones (*Arenaria interpres*), gulls, others	Delaware Bay	Spring	A few weeks; peak in spring, high tides	Myers (1986), Castro and Myers (1993), Clark et al. (1993), Botton and Loveland (1993), Tsipoura and Burger (1999), Baker et al. (2004)
Amphipod (*Corophium volutator*)	Semipalmated sandpipers, semipalmated plovers (*Charadrius semipalmatus*), least sandpipers Calidris *minutilla*), short-billed dowitchers (*Limnodromus griseus*)	Bay of Fundy	Summer	A few weeks	Hicklin and Smith (1979, 1984); Hicklin et al. (1980), Murdoch et al. (1986), Peer et al. (1986), Hicklin (1987), Dunn et al. (1988), Wilson (1990), Matthews et al. (1992), Hamilton et al. (2003)

(Tsipoura and Burger 1999). Populations of the subspecies of red knot (*Calidris canutus rufa*) that stop in Delaware Bay appear to track the abundance of horseshoe crabs and have recently declined in abundance, reportedly in response to a decline in the crabs (Baker et al. 2004; Morrison et al. 2004).

Hundreds of thousands of shorebirds on southward migration land on the shores of the Bay of Fundy; most of the world's population of semipalmated sandpipers (*Calidris pusilla*) stops here (Peer et al. 1986; Hicklin 1987), feeding heavily on *Corophium* amphipods. The tube-dwelling amphipods are present year-round, but the number of large, mature individuals peaks when the shorebirds are passing though. Migrants are generally present for 2–8 weeks; individual semipalmated sandpipers stay for an average of 15 days (Hicklin 1987). Sandpipers with high fat content stay on this feeding ground for less time than those with low fat content, indicating the importance of this stopover site for continued migration (Dunn et al. 1988). A sandpiper can double its weight in 2–3 weeks of feeding on amphipods, before migrating 4,000 km nonstop to South America (Hicklin and Smith 1984; Wilson 1990). Body-fat levels of semipalmated sandpipers were correlated with the probability of survival and their annual return from migration in Massachusetts (Pfister et al. 1998). Bird predation is so intense that it contributes to a seasonal decline in the abundance of large amphipods (Hicklin et al. 1980; Murdoch et al. 1986; Peer et al. 1986; Matthews et al. 1992). Populations of *Corophium* on some beaches have collapsed, causing the migrants to move to other foraging sites (Hamilton et al. 2003).

We also note some nonmarine studies indicating fitness consequences of short-term use of prey, because there are so few cases in marine systems. For example, weight gain and survival of young chicks of the European golden plover (*Pluvialis apricaria*) were associated with the pulsed abundance of emerged crane fly adults (Pearce-Higgins and Yalden 2004). Migrating insectivorous warblers (Parulidae) at some locations in the Great Lakes capitalize on emerging swarms of midges and the spiders that also exploit the midge swarms. Warblers that stay to breed in the area continue to exploit midges and the later-emerging mayflies and have better body condition and higher breeding success than those in more inland sites without these resources (Smith 2003). Wilson's phalaropes (*Phalaropus tricolor*) stop over in saline lakes in the western U.S. on their southward migration, feeding intensively on brine shrimp (*Artemia*) and brine flies (*Ephydra*) for a few weeks, while laying down large quantities of fat for their long migration to southern South America (Jehl 1988).

The case studies presented in Table 1 are interactions that usually occur annually. Regular exploitation of short-term prey pulses depends on the predictability of the prey in time and space and the ability of predators to accommodate variation in occurrence and distribution of the prey. It is therefore important to know how variable such short-term prey resources are. Some prey populations, like the amphipods in the Bay of Fundy, are present year-round but have peaks of abundance that are exploited by predators on a short-term basis. Others, such as spawning snappers or herring (Table 1), are typically available to predators only for brief periods each year. Still others, including the brine shrimp and brine flies of alkali lakes, are present all summer and used by many predators but exploited by the migrating phalaropes for only a short time.

We have found only two data sets, however, that document variation in prey availability over relatively long time periods. The timing of peak outmigrations of pink salmon (*Oncorhynchus gorbuscha*) fry at two sites in Southeast Alaska varied by as much as 1–2 months, and the duration of the peak varied from a few days to about 6 weeks (Olson and McNeil 1967; pers. comm., S. G. Taylor, Auke Bay Laboratory, Juneau AK). Although this resource is quite predictable in space, its unpredictability in time is considerable, which must affect the ability of predator populations to exploit it.

In this paper, we develop the second example in more detail: Pacific herring (*Clupea pallasii*) is a widespread forage fish, preyed upon by numerous marine predators and, because of its commercial value, far better studied than other forage fishes in the North Pacific. Much remains to be learned about the interactions of this prey species with its predators. However, we think it is valuable to synthesize what is known and suggest further research.

Spawning herring as a short-term resource

Although herring can be important prey for some predators at any time of year, we focus here on their spawning aggregations and spawned eggs. Pacific herring in North America range from California to the Arctic Ocean and, in Asia, south to northern Japan (Haegele and Schweigert 1985; Hay 1985). Groups of spawning herring are densely aggregated, often involving many millions of adult fish, with activity sometimes spread over several kilometers of shore (Blaxter and Hunter 1982).

Pacific herring spawn mainly in inlets, sounds, and bays that are somewhat sheltered from the open ocean. Eggs are usually deposited in intertidal and subtidal zones to a depth of about 15 m, with the highest densities usually at depths <5 m (Haegele and Schweigert 1985; Gerke 2002). Spawning substrates are commonly algae and sea grasses, but also rock and sand (Haegele and Schweigert 1985). In general, herring spawn as early as December in California and as late as June in northwestern Alaska, with occasional spawning events beyond those months (Haegele and Schweigert 1985; Hay 1985). These seasonal differences obviously would have differing implications for the seasonal exploitation patterns and ecology of predators in different areas.

Spawning in any given area usually occurs within a span of 3–6 weeks and may occur in two or more separate waves of activity (Haegele and Schweigert 1985; Hay 1985). The eggs hatch in 1.5–3 weeks (Outram and Humphreys 1974; Wespestad and Barton 1979; Palsson 1984). Although some observers report that predators seem to prefer freshly deposited eggs, Bishop and Green (2001) found no such preference. Commonly, for a given spawning episode, eggs would be available for less than 6 weeks.

Female herring produce tens of thousands of eggs (Outram and Humphreys 1974; Hay 1985); large females produce more and larger eggs than small females (Hay 1985, Ware 1985). Egg sizes range from about 0.8 mg to about 1.5 mg wet mass (Hay 1985), and the average energy content of one egg is 8.1 J (SD ± 0.9) (Paul and Paul 1999). The average energetic content of ripe Pacific herring ovaries from Prince William Sound, Alaska, is 5.7 kJ/g wet mass (Paul et al. 1996), or 23.86 kJ/g dry mass (SD ± 1.19) (Paul and Paul 1999). Whole ovaries range from 50 kJ to 300 kJ wet wt, and spawning female herring may expend up to 97% of the energy in the ovary. For the closely related Atlantic herring (*C. harengus*), female gonads contained up to about 25% lipid, chiefly triacylglycerols (Henderson and Almatar 1989).

Egg mortality is high (e.g., Palsson 1984; Rooper 1996). Principal abiotic causes of mortality include desiccation of intertidal eggs, suffocation of eggs deposited in thick layers (e.g., over 100 eggs thick, and over a million eggs/m^2), strong wave action, and deposition at excessive depths (Outram and Humphreys 1974; Blaxter and Hunter 1982; Haegele and Schweigert 1985; Hay 1985; Rooper 1996). Fish (including herring) and invertebrates can be important predators (Wespestad and Barton 1979; Palsson 1984; Hay 1985; Haegele 1993b; Rooper 1996). Most studies of egg predation, however, have focused on birds (see below). Bird-exclusion experiments commonly have failed to account for predation by fish and invertebrates and seldom accounted for other sources of mortality, so the effect of avian predation has been overestimated in many cases. In any case, it is thought that mortality of larvae rather than eggs may determine year-class abundance (Lasker 1985).

The ability of predators to digest and assimilate nutrients from herring eggs is, apparently, not yet known. However, several studies of digestibility (assimilation efficiency) or digestive efficiency of pinnipeds eating herring yielded values ranging from 84 to 94% and 93% to 95% respectively (reviewed by Rosen and Trites 2000). For seabirds, assimilation efficiency on fish diets is estimated to be 75–85%, increasing with higher lipid content of prey (Furness and Tasker 1997).

Major predators at herring spawns

At least 25 vertebrate species have been observed to occur in relative large numbers at herring spawns, foraging on spawning herring and/or their eggs (Table 2); most of these counts are snapshots in time, not accounting for turnover of animals that might move in and out of the foraging area, and so may be underestimates. The species found most regularly and in the largest numbers at spawning events are birds. Gulls, shorebirds, geese, and crows typically feed on eggs exposed at low tide (Munro and Clemens 1931; Vermeer 1981; Norton et al. 1990; Vermeer et al. 1992); scoters and diving ducks feed subtidally (but Haegele 1993a reported that scoters in one study area did not feed on herring spawn). Gulls (*Larus* spp.), murres (*Uria aalge*), western grebes (*Aechmophorus occidentalis*), and mergansers (*Mergus serrator*) often eat both eggs and fish, but bald eagles, cormorants (*Phalacrocorax* spp.), and loons (*Gavia immer*) typically forage on the fish (Table 2). Mammals recorded foraging at herring spawning sites are gray whales (*Eschrichtius robustus*; Haegele and Schweigert 1989, pers. comm., J. Straley, Sitka AK), humpback whales (*Megaptera novaeangliae*; Straley 1990, pers. comm., J. Straley, Sitka AK), killer whales (*Orcincus orcas*; Van Opzeeland et al. 2005), and Steller sea lions (Womble et al. 2005).

Because herring spawn in spring, they offer a rich food source for predators just emerging from winter (when food is often limited and energy costs are high), preparing to migrate or en route, and preparing to breed. Most of the published information about predators comes from more southern latitudes (Table 2). Some predators at a given location are mostly wintering birds (goldeneyes and bufflehead (*Bucephalus* spp), harlequin (*Histrionicus histrionicus*), Western grebe), some may be mixed populations of wintering or migrating birds (brant (*Branta bernicla*), Thayer's gull, mergansers), and others are migrants (scoters (*Melanitta* spp.), shorebirds). The status of still others is not entirely clear: some are probably regional and local breeding birds (e.g., northwestern crow, *Corvus caurinus*). In Southeast Alaska, we have seen hundreds of bald eagles fishing at herring runs in May; these congregations are probably composed of both local and regional residents and migrants.

The nutritional value, high density, and seasonal timing of the herring runs indicate

Table 2 Predators on spawning herring and herring eggs

Species	Location	Reference
Gulls		
Mew gull (*Larus canus*)	OR, WA, SoG, PWS	Munro and Clemens (1931), Grass (1973), Bayer (1980), Vermeer (1981), Bishop and Green 2001
Glaucous-winged gull (*L. glaucescens*)	OR, SoG, WV, PWS	Munro and Clemens (1931), Outram (1958), Bayer (1980), Vermeer (1981), Vermeer and Morgan (1992), Haegele and Schweigert (1989), Bishop and Green (2001), Pers.comm., M. A. Bishop, Prince William Sound Science Center, Cordova AK
Thayer's gull	SoG, WV	Munro and Clemens (1931), Vermeer and Morgan (1992), Haegele and Schweigert (1989)
'Herring gull' (*L. argentatus*)	WV	Outram (1958) (could be Thayer's gull); Haegele (1993a), Haegele and Schweigert (1989)
Sea ducks		
Surf scoter (*Melanitta perspicillata*)	OR, WA, SoG, WV, QC, PWS	Munro and Clemens (1931), Cleaver and Franett (1946), Bayer (1980), Haegele and Schweigert (1989), Vermeer et al. (1992, 1997), Bishop and Green (2001)
White-winged scoter (*M. fusca*)	SoG, QC	Munro and Clemens (1931), Vermeer (1981), Vermeer and Bourne (1983), Vermeer et al. (1997)
Black scoter (*M. nigra*)	QC	Vermeer et al. (1997)
Diving ducks		
Harlequin	SoG, WV, QC	Haegele and Schweigert (1989), Haegele (1993a), Vermeer et al. (1997), Rodway and Cooke (2001, 2002), Rodway et al. (2003)
Greater scaup (*Aythya marila*)	OR, WA, SoG + Fraser R.	Munro and Clemens (1931), Cleaver and Franett (1946), Bayer (1980), Vermeer (1981), Vermeer et al. (1997)
Long-tailed duck (*Clangula hyemalis*)	SoG, QC	Munro and Clemens (1931), Vermeer (1981), Haegele (1993a)
Common goldeneye (*Bucephala clangula*)	SoG QC	Munro and Clemens (1931), Vermeer (1981), Haegele (1993a)
Barrow's goldeneye (*B. islandica*)	SoG, WV	Vermeer (1981), Haegele and Schweigert (1989), Vermeer and Morgan (1992), Haegele (1993a)
Bufflehead (*B. albeola*)	OR, SoG, WV, QC	Munro and Clemens (1931), Bayer (1980), Vermeer (1981), Haegele and Schweigert (1989), Haegele (1993a), Vermeer et al. (1997)
Red-breasted merganser**	SoG	Munro and Clemens (1931), Vermeer (1981), Haegele (1993a)
Geese, dabblers		
Brant	OR, SoG, QC	Bayer (1980), Vermeer et al. (1997), Haegele (1993a), Sullivan et al. (2002)
Canada goose (*B. canadensis*)	SoG, WV	Haegele and Schweigert (1989), Haegele (1993a)
Mallard (*Anas platyrhynchus*)	SoG	Haegele (1993a)
Cormorants, loons, grebes		
Brandt's cormorant*** (*Phalacrocorax penicillatus*)	SoG, WV	Vermeer (1981), see also Vermeer (1983), Haegele and Schweigert (1989)
Pelagic cormorant*** (*P. pelagicus*)	SoG, WV	Munro and Clemens (1931), Vermeer (1981), Haegele and Schweigert (1989)
Western grebe**	SoG	Vermeer (1981), see also Vermeer (1983)
Common loon***	SoG	Sullivan et al. (2002)
Shorebirds, alcids, coot		
Common murre **	SoG	Munro and Clemens (1931)

Table 2 continued

Species	Location	Reference
Surfbird (*Aphriza virgata*)	PWS	Norton et al. (1990), Bishop and Green (2001)
Black turnstone (*Arenaria melanocephala*)	WA, PWS	Grass (1973), Norton et al. (1990), Bishop and Green (2001)
American coot (*Fulica americana*)	OR	Bayer (1980)
Eagles		
Bald eagle	SoG, Juneau AK	Haegele (1993a), personal observations
Passerines		
Northwestern crow	SoG, WV	Haegele and Schweigert (1989), Haegele (1993a)
Mammals		
Steller sea lion***	Southeast Alaska	Womble et al. (2005)
Humpback whale***	Prince of Wales Is.	Pers. comm., John Church, Juneau AK (about 30 whales present)

This list contains only species reported to occur in numbers >100 animals in at least one site, with the exception of humpback whales, which were seen in lesser numbers but are included because of the large biomass represented; many other species may be present in smaller or unstated numbers. Species numbering in the thousands in at least one site are in bold font. ** Consumers of both fish and eggs; *** Consumers of fish primarily. Run timing was late February through March in OR, WA, and southern BC, but April in south-central Alaska. Abbreviations for locations: WV = West Vancouver Island, QC = Queen Charlotte Islands, SoG–Strait of Georgia, PWS = Prince William Sound, WA = Washington, OR = Oregon

seasonally important opportunities for predators to obtain energy and nutrients relatively easily and quickly. That so many predators often gather at herring runs strongly suggests that the runs are important to predator biology.

Predictability of herring spawns

Resource predictability constrains the patterns of exploitation by predators, because predators may be able to exploit (or to profit most from exploiting) resources only within a certain distance or only at certain times. It is therefore useful to understand the temporal and spatial scale of variation in resource availability, as a background for exploring the relationship of predators to the resource.

We examined the predictability of herring spawning runs in time and space, using a remarkable data set available for the British Columbia coastline. The Department of Fisheries and Oceans (DFO) in BC has documented the timing and magnitude of herring spawn for many decades along the BC coast. The coast is divided into six regions (Fig. 1), each consisting of a number of sections (9–28 with reported data) of differing size. The dataset covers most sections for most years between the late 1930s and the present (http://www.pac.dfo-mpo.gc.ca/sci/herring/herspawn/pages), although a previous printed summary through 1989 is also available (Hay et al. 1989). However, our analyses are based on the earlier print versions, which are adequate for purposes of discussion and exploration of the temporal and spatial scales of variation in herring spawning.

We focused our examination at two spatial scales: region and section, but for some exploratory analyses we consider clusters of adjacent sections. The DFO authors also reported that very local variation occurs on a scale of <5 km, which was not examined here. We considered seasonal timing and magnitude (SI = spawn index in square meters of spawn) of the spawning runs, as well as the annual reliability of the runs. We defined large runs as those having a SI $>$ 100,000 m^2, and medium runs with SI > 10 000 m^2. The usual run size per section ranged from very small to large in every region, and run size (five categories, defined by DFO) is positively related to year-to-year constancy (three categories, defined by DFO) ($r = 0.61$, $P = 0.000$). Most runs occurred in March and April, with May and June runs in a few areas. In general, runs occurred somewhat later at higher latitudes, but there was considerable overlap in run timing among regions (Fig. 2).

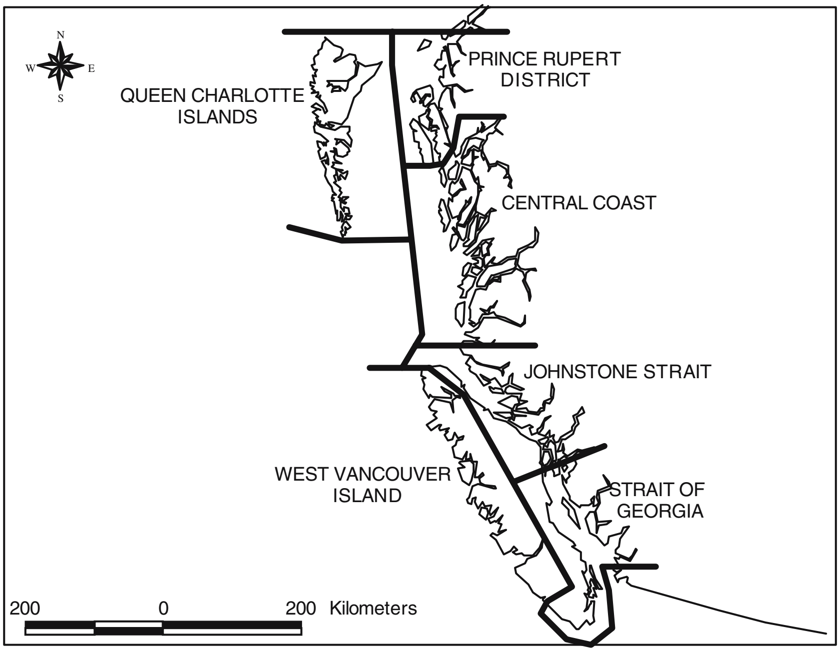
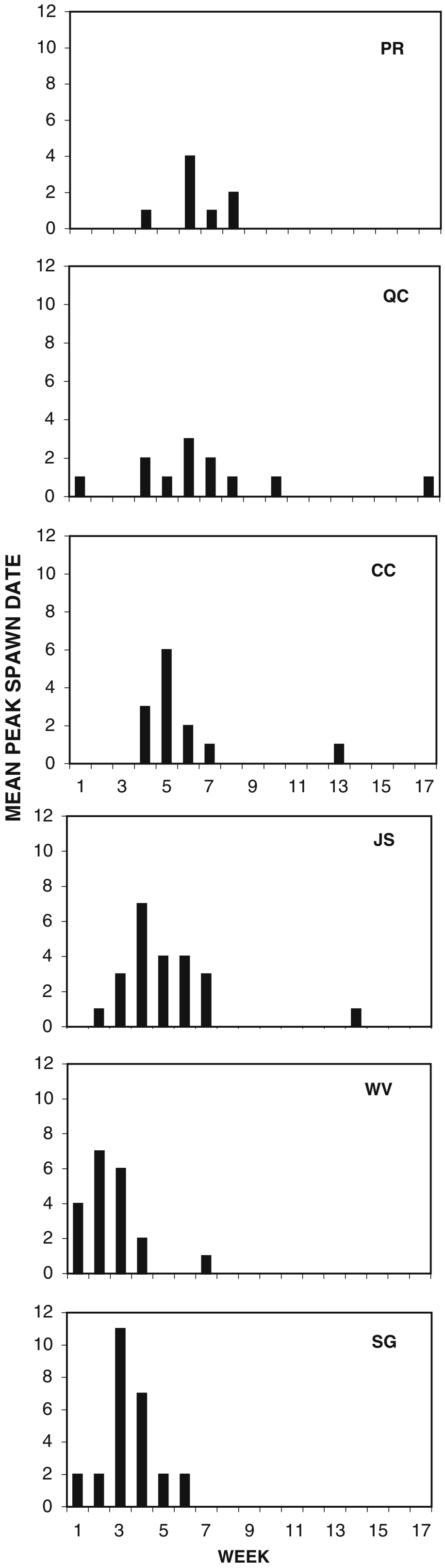


Fig. 1 Regional divisions of herring spawning assessments by DFO in British Columbia, used in this study

At the level of the region, reliability, magnitude, and timing of spawning runs were quite variable. Each region had runs in up to 70–92% of the sections, indicating widespread spawning activity in many years (Table 3; column A). The average frequency of spawning runs per section ranged from 52% to 72% of years in the six regions (Table 3; column B). Regionally, on average, 42–61% of years had runs with a medium spawn index, and 10–34% of years had a large spawn index (Table 3; columns C,D). Large runs occurred in at least 78% of years somewhere in all regions and every year in three regions (Table 3; column E). The regions did not necessarily vary synchronously through the years: for example, the number of large runs in the Strait of Georgia was notably higher in some years than in any other region. However, there was a general tendency for spawn abundance to be positively correlated among regions (but not necessarily among sections within regions; Hay and Kronlund 1987). Temporal variation was marked: within a region (over all sections), the mean date of the earliest spawning activity differed among years by 40–61 days, and the mean dates of spawning peaks differed by up to four weeks among regions (Table 3; columns F,G; Fig. 2). The maximum duration of each spawning event was 5–8 days, on average, but when multiple spawning events occurred, duration of spawning activity ranged up to three or four weeks (Table 3; column H).

At the level of the section, variation was still more pronounced (ranges in Table 3). Some sections had spawning runs less than three times in 40–50 years, while others lacked runs only once or twice or not at all (Table 3; column B). The frequency of medium and large spawn indices ranged widely from section to section (Table 3; columns C,D). The average difference in the dates of the earliest spawning activity in each section ranged up to 61 days; in some sections annual run timing differed by over 100 days (Table 3; column F). Mean dates of spawning peaks, over all years, varied among sections by about 6 weeks (Strait of Georgia) to about 16 weeks (Queen Charlottes) in the different regions (Table 3; column G; Fig. 2). Even the 'best' spawning sections (large runs in at least 85% of years, $n = 14$ sections) varied markedly in run timing among years: for example, the date of earliest spawn within these sections varied by 23–86 days.

Most predators are mobile and capable of moving at least to adjacent sections if the runs fail in one place. Therefore, we also examined a sample of clusters of adjacent sections, in a



◀**Fig. 2** Variation in mean peak spawning times for herring among and within regions on the coast of British Columbia. PR = Prince Rupert, QC = Queen Charlotte Islands, CC = Central Coast, JS = Johnstone Strait, WV = West Vancouver Island, SG = Strait of Georgia

preliminary exploration at a spatial scale larger than a single section. We arbitrarily selected one section (with medium or large runs in at least 85% of years) per region, using the data only from every fifth year (n = 10 yrs in most cases). The probability that a section adjacent to the focal section would have a large spawning run in some year ranged from 5% (Prince Rupert) to 45% (Strait of Georgia), and the probability of at least a medium run ranged from 35% (Prince Rupert) to 50% (Strait of Georgia). The mean timing of peak runs within the focal sections varied from 17 days to 46 days among years. On average, the timing of adjacent sections (assuming a run occurred) ranged from about 43 days earlier to about 15 days later, with a difference of less than three days in three cases. So, on average, a predator in the focal area might find another run (of unspecified size) nearby within 3 days if it were sufficiently mobile, but might miss a run altogether or have to wait about 2 weeks.

Thus, both the location and timing of herring spawning varied on a scale that is likely to be important to consumers. Regionally, a large spawning run was usually present every year. Some sections exhibited high levels of annual reliability, while others were sporadic. Sections with high annual reliability tended to have runs of greater magnitude, although the scatter in this relationship was marked. Timing of the run in a section often varied as much as 2–3 months from year to year.

From a predator's perspective, a sufficiently mobile predator could reliably find quantities of spawning herring somewhere in a region every year, but less mobile predators may have difficulty in compensating for local variability in both magnitude and timing. The most mobile predators are likely to be birds (e.g., gulls and eagles) that forage on herring before the nesting season; once nesting begins, their search areas become more restricted because the parent birds then become central-place foragers. However, some

Table 3 Variation in magnitude and timing of herring spawn on the British Columbia coast

Region*	**A**. Max. % of sections with runs in any year	**B**. Ave. % of years with spawn[a] (range)	**C**. Ave. % of years with medium spawn index[a] (range)	**D**. Ave. % of years with large spawn index[a] (range)	**E**. Regional % of years with large runs	**F**. Ave. variation of early spawn date[a] (range)	**G**. Ave. peak week[a,b] (range)	**H**. Ave. max. duration of spawn[a] (range)
QC	92	72 (14–100)	58 (2–100)	23 (0–87)	84	44d (20–91)	6 (1–17)	6d (1–18d)
PR	88	61 (4–100)	61 (18–100)	34 (0–98)	100	61d (2–86)[c]	6 (4–14)	5d (1–12d)
CC	83	66 (14–100)	49 (2–100)	19 (0–74)	92	40d (11–77)	5 (4–13)	8d (2–21d)
JS	78	66 (4–100)	46 (0–88)	10 (0–42)	78	48d (21–111)	5 (2–14)	5d (1–13d)
SG	70	52 (0–100)	42 (0–100)	23 (1–94)	100	51d (20–101)	3 (1–6)	8d (1–28d)
WV	81	68 (4–100)	50 (2–100)	20 (0–92)	100	52d (8–86)[c]	2 (1–7)	6d (1–15d)

QC = Queen Charlottes, PR = Prince Rupert/North Coast; CC = Central Coast; JS = Johnstone Strait/Lower Central Coast; SG = Strait of Georgia; WV = West Vancouver Island

[a] Average over all sections per region; [b] weeks numbered starting with 1 March; [c] smallest values from sections with rare spawns

birds, including harlequin ducks, appear to have area-restricted search patterns even in winter (Rodway et al. 2003), which would limit their ability to focus on herring as prey. Mammals likewise vary in their apparent ability to track a shifting prey concentration. Pinnipeds sometimes locate their haulouts close to winter herring aggregations (Womble and Sigler in press), as well as eulachon runs in spring (Womble et al. 2005), but they may be less mobile than whales because of their terrestrial base at haulouts and central-place foraging strategy. Although harbor seals (*Phoca vitulina*) typically stay within 25 km of their haulout site, some harbor seals in Prince William Sound traveled up to 125 km to the Copper River Delta in May when eulachon spawn there (Lowry et al. 2001). The same species of predator might need to adopt differing strategies in different areas, depending not only on the patterns of variation in herring spawn but also the reproductive status of the individual predator. For example, juvenile Steller sea lions typically make foraging trips within 25 km of the haulout (Loughlin et al. 2003; Raum-Suryan et al. 2004), whereas adult sea lions make longer trips (Merrick and Loughlin 1997). If adult females are still provisioning dependent pups, then the benefits of finding a herring run may be offset by the cost of increased travel at greater distances from the haulout. In general, one would expect that the less mobile predators would be more likely to seek alternative prey, or that they would suffer greater negative effects on breeding and survival, when herring become less available.

Catastrophic changes in herring populations

In addition to annual variations, herring populations sometimes crash precipitously and may be long in recovering. Prey-fish populations vary in response to both external and intrinsic factors (e.g., Lasker 1985), but many herring stocks have crashed, primarily because of overfishing by humans[1] (e.g., Rounsefell and Dahlgren 1935; Lillegård et al. 2005). Population collapses can be followed by changes of seasonal movement

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[1] Moulton (1999) Review of Lynn Canal herring. MJM Research, 1012 Shoreland Drive, Lopez Island, WA.

patterns (e.g., Similä et al. 1996) or by prolonged absences of spawning aggregations from traditional sites. For example, a major herring stock in the Hokkaido and Sakhalin Island area has not recovered from a collapse that occurred more than 50 years ago (Hay et al. 2001). Several stocks in Southeast Alaska decreased so much that they are no longer commercially profitable (e.g., Rounsefell and Dahlgren 1935). The fishery in Lynn Canal in Southeast Alaska was reduced to below acceptable threshold levels by 1982 and the expanse of shoreline spawn is still limited to a small portion of the former extent.[1]

Herring on the British Columbia coast comprise a metapopulation, with dispersal among areas, and the amount of dispersal varies with population size and climatic regime.[2] Nevertheless, recolonization of sections that lost their herring stocks took an average of 11 years; some sections were recolonized in less than 5 years, but others had not been recolonized for 35 years.[3] Over half the sections lost spawning events during a period of 60 years, and only 53% of recolonization attempts were successful.[2] As expected, loss of spawning was less common in areas with large amounts of spawning habitat and larger spawning episodes.[2]

In addition to overharvesting, other catastrophic events may impair herring stocks and herring spawning aggregations. For example, the Exxon Valdez oil spill in 1989 in Prince William Sound, Alaska, caused oil-related impacts on both herring eggs and larvae (Hose et al. 1996; McGurk and Brown 1996; Norcross et al. 1996; Carls et al. 2002). After that oil spill Paul et al. (1996) estimated that the amount of energy contributed to the ecosystem by herring eggs decreased from 68×10^9 kJ in 1988 to 10×10^9 kJ in 1995, with implications not only for herring recruitment but also for predator species that consume herring in Prince William Sound. The decrease in herring biomass in Prince William Sound was accompanied by a continuing decline of Steller sea lions that began in the mid-1970's (Calkins et al. 1994; Loughlin et al. 1992). Harbor seals also experienced an overall population reduction of 63% from 1984 to 1997 in Prince William Sound (Frost et al. 1999; VerHoef and Frost 2003). Herring is an important prey item for both Steller sea lions and harbor seals in Prince William Sound (Pitcher 1980, 1981; Thorne 2005). It seems likely that predators of spawning herring and their eggs would likewise be negatively affected. Given the holarctic distribution of herring, declines in herring stocks have the potential to dramatically affect numerous predator populations that rely upon herring throughout the northern hemisphere.

General discussion

Variation in populations of prey fish such as herring has implications for many aspects of predator biology, as well as management and conservation. Although we lack any measure of fitness consequences for predators that exploit spawning runs of herring, we can relate what we have learned about herring to other general questions.

Energy storage

Capital breeding (using stored energy and nutrients for a costly activity), in contrast to income breeding (using resources garnered daily at the site of activity), is thought to be most beneficial when food resources in the breeding environment are not predictable, when food or foraging time are limited, or foraging is particularly risky (Jönsson 1997). There are costs associated with fat storage in birds, such as increased costs of locomotion (e.g., Burns and Ydenberg 2002; Guillemette and Ouellet 2005, but see also Kvist et al. 2001), which may be reduced by dimishing the size of organs not essential to long-distance flights (e.g., Piersma 1998). Similarly, tradeoffs between feeding now and feeding later have been suggested for marine mammals (e.g., Rosen and Trites 2002). Many organisms may lie on a gradient between income

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[2] Ware DM, Schweigert (2002) Metapopulation dynamics of British Columbia herring during cool and warm climate regimes. DFO Canadian Science Advisory Secretariat Research Document 2002/207. http://www.dfo-mpo.gc.ca/Csas/.

[3] Ware, DM, Tovey C (2004) Pacific herring spawn disappearance and recolonization events. DFO Canadian Science Advisory Secretariat Research Document 2004/008. http://www.dfo-mpo.gc.ca/Csas/.

and capital breeding (Thomas 1988, cited in Meijer and Drent 1999), and some consumers may be capital breeders for one nutrient but income breeders for another (Casas et al. 2005).

Many species known to forage at herring runs are migrating or about to migrate, and prey consumption may contribute chiefly to fueling the costs of migration. At least in some cases, higher body-fat levels appear to increase annual survival of migrants (Pfister et al. 1998). Birds breeding at high latitudes are commonly income breeders, depending mainly on resources garnered on the breeding ground, although large-bodied species and early nesting individuals use some stored resources (Meijer and Drent 1999; Klaassen et al. 2001; Morrison and Hobson 2004). Capital breeding may be more common among birds that are not long-distance migrants but generally make regional and local movements; for example, six species of fish-eating seabirds in western Alaska failed to lay eggs at all, at certain sites and in certain years, suggesting that nearby resources were inadequate to achieve breeding condition (Dragoo et al. 2004). We suggest that if herring runs are important to capital breeders, those species are more likely to be regional or local breeders than long-distant migrants.

Among the mammalian predators at herring runs, Steller sea lions make regional movements from feeding grounds to breeding rookeries. Males are capital breeders, fasting for weeks while on the rookeries (Gentry 1970; Sandegreen 1970). Female sea lions fast for shorter periods of time (5–13 days) and start foraging again a few days after their pups are born (Sandegreen 1970), and so are partly capital breeders. Humpback whales forage all summer at high-latitude feeding grounds, and then the breeders move to Hawaii to calve and mate; they may spend energetic capital for the mating season in the south but become income breeders while feeding calves in northern waters.

Specialized foraging methods

Prey aggregations provide an opportunity for the development of specialized foraging methods. A common feature of avian aggregations at spawning runs is a high level of piracy (birds stealing or attempting to steal food from each other). In Southeast Alaska, piracy was a common means of foraging for gulls (Willson and Marston 2002) and bald eagles (pers. obs.) congregated at eulachon runs. Similarly, at a herring run in Oregon, brants pirated eggs from coots, wigeon (*Anas americana*) from coots and scaup (*Aythya* sp.), bufflehead from scaup, and gulls from other species and each other (Bayer 1980).

Highly aggregated prey also provide an opportunity for cooperative foraging by multiple predators, as reported for humpback whales (Jurasz and Jurasz 1979, pers. obs.) and killer whales (*Orcinus orca*) foraging on winter (Similä and Ugarte 1993) and spring-spawning herring (Van Opzeeland et al. 2005). Steller sea lions sometimes forage cooperatively for prespawning eulachon, by forming long lines composed of dozens or even hundreds of sea lions, and chasing the prey from one side of a bay to the other (Gende et al. 2001; Sigler et al. 2004) and also for overwintering herring (Thomas and Thorne 2001). In eastern Antarctica, 150–200 crabeater seals (*Lobodon carcinophagus*) have been observed synchronously diving and surfacing near aggregations of patchily distributed krill (*Euphausia superba*; Gales et al. 2004).

Research needs

Clearly, there are many lacunae in our knowledge of exploitation of short-term prey. It is likely that there are many other examples to be discovered, which would have important implications both for understanding species' ecology and for conservation and management. Predator diets and activity must be sampled on a time and spatial scale that reflects short-term exploitation; for example, Steller sea lions in northern Southeast Alaska forage heavily on eulachon for perhaps 2 weeks, and sometimes establish terrestrial haulouts nearby; scat samples only from the breeding rookeries or the winter haulouts would fail to detect this altogether (Womble et al. 2005). The fitness consequences of exploiting short-term prey, including what happens when the prey population crashes or moves, are seldom known, so we cannot usually measure the effects of anthropogenic or other disturbances.

It should be possible to model the potential effects of prey crashes on different types of predator populations. Dependence on some usually reliable pulsed prey creates the accompanying risk of catastrophic crashes if that prey suddenly disappears. However, the most valuable models would incorporate the relevant and difficult-to-obtain biological detail (Maurer 1990) needed to tie the model to reality, including information on prey assessment, trade-offs among different dietary inputs and predator activities, risk sensitivity and responses to prey variability, and interactions among the factors that affect decision-making by the predator (Stephens 1990). A related consideration is change in prey quality, which would alter the value to the predator of consuming a particular prey, no matter how abundant it might be. For example, birds feeding on *Corophium* amphipods in southern Canada were found to contain high levels of industrial contaminants (Vermeer 1992), suggesting that there may be a cost to consuming this prey in some areas.

Because prey fish such as herring often move seasonally (Carlson 1980; Corton 2002), human harvesting in one area may affect predators in other areas. Therefore management plans that include consideration of wildlife would need to account for the mobility of prey populations, but tracking mobile prey at sea has always been a difficult proposition.

For most of this essay, we have been concerned with the relationship of predators to predictability of their prey. However, there are also important considerations from the perspective of the prey. Very early and very late spawning runs or areas with highly variable run timing, for example, might escape the heaviest predation. If it is true that variable prey populations are harder for predators to exploit than more predictable prey populations, then whatever the proximate causes of the variation, the ultimate consequences of unpredictability could be greater survival of the prey. For species with metapopulation structure (with dispersal among metapopulation segments), such as herring, and for which the less variable, more 'reliable' populations receive very heavy predation (by humans or others), the variable populations might contribute more significantly than otherwise expected to maintenance of the metapopulation—although evidently not enough to allow quick replacement of catastrophically diminished stocks. We propose that the apparently 'unreliable' prey populations in a metapopulation may have significant management and conservation value in the long run.

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References

Baker AJ, González PM, Piersma T, Niles LJ, de Lima Serrano do Nascimento I, Atkinson PW, Clark NA, Minton CDT, Peck MK, Aarts G (2004) Rapid population decline in red knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. Proc Roy Soc Lond B 271:875–882

Bayer RD (1980) Birds feeding on herring eggs at the Yaquina estuary, Oregon. Condor 82:193–198

Bishop MA, Green SP (2001) Predation on Pacific herring (*Clupea pallasii*) spawn by birds in Prince William Sound, Alaska. Fisher Oceanogr 10(Suppl. 1):149–158

Blaxter JHS, Hunter JR (1982) The biology of the clupeoid fishes. Adv Mar Biol 20:1–223

Botton ML, Loveland RE (1993) Predation by herring gulls and great black-backed gulls on horseshoe crabs. Wils Bull 105:518–521

Burgner RL (1991) Life history of sockeye salmon (*Oncorhynchus nerka*). In: Groot C, Margolis L (eds) Pacific salmon life histories. University of British Columbia, Vancouver, BC, pp 1–117

Burns JG, Ydenberg RC (2002) The effects of wing loading and gender on the escape flights of least sandpipers (*Calidris minutilla*) and western sandpipers (*Calidris mauri*). Behav Ecol Sociobiol 52:128–136

Calkins D, Becker E, Spraker T, Loughlin T (1994) Impacts on Steller sea lions. In: Loughlin TR, (eds) Maine mammals and the Exxon Valdez. Academic Press, San Diego, CA, pp 119–139

Carls MG, Marty GD, Hose JE (2002) Synthesis of the toxicological impacts of the *Exxon Valdez* oil spill on Pacific herring (*Clupea pallasii*) in Prince William Sound, Alaska, U.S.A. Can J Fish Aquat Sci 59:153–172

Carlson R (1980) Seasonal distribution and environment of Pacific herring near Auke Bay, Lynn Canal, southeastern Alaska. Trans Am Fish Soc 109:71–78

Casas J, Pincebourde S, Mandon N, Vannier F, Poujol R, Giron D (2005) Lifetime nutrient dynamics reveal simultaneous capital and income breeding in a parasitoid. Ecology 86:545–554

Castro G, Myers JP (1993) Shorebird predation on eggs of horseshoe crabs during spring stopover on Delaware Bay. Auk 110:927–930

Clark KE, Niles LJ, Burger J (1993) Abundance and distribution of migrant shorebirds in Delaware Bay. Condor 95:694–705

Cleaver FC, Franett DM (1946) The predation by sea birds upon the eggs of the Pacific herring (*Clupea pallasii*) at Holmes Harbor during 1945. Department of Fisheries, Division of Scientific Research, State of Washington, Biological Report 46B

Corton A (2002) The role of 'conservatism' in herring migrations. Rev Fish Biol Fisher 11:339–361

Dickerson BR, Quinn TP, Willson MF (2002) Body size, arrival date, and reproductive success of pink salmon, *Oncorhynchus gorbuscha*. Ethol Ecol Evol 14:29–44

Dragoo DE, Byrd GV, Irons DB (2004) Breeding status, population trends and diets of seabirds in Alaska, 2002. U. S. Fish and Wildlife Service Report AMNWR 04/15

Dunn PO, May TA, McCollough MA, Howe MA (1988) Length of stay and fat content of migrant semipalmated sandpipers in eastern Maine. Condor 90:824–835

Frost KJ, Lowry LF, VerHoef JM (1999) Monitoring the trend of harbor seals in Prince William Sound, Alaska after the Exxon Valdez oil spill. Mar Mammal Sci 15:494–506

Furness RW, Tasker ML (1997) Seabird consumption in sand lance MSVPA models for the North Sea, and the impact of industrial fishing on seabird populations dynamics. In: Forage fishes in marine ecosystems. University of Alaska Sea Grant College Program Report No. 97–01, pp 147–169

Gales NJ, Fraser WR, Costa DP, Southwell C (2004) Do crabeater seals forage cooperatively?. Deep-Sea Res II 51:2305–2310

Gende SM, Womble JN, Willson MF, Marston BH (2001) Cooperative foraging by Steller sea lions (*Eumetopias jubatus*). Can Field-Nat 115:355–356

Gende SM, Quinn TP, Willson MF, Heintz R, Scott TM (2004) Magnitude and fate of salmon-derived nutrients and energy in a coastal stream ecosystem. J Freshwater Ecol 19:149–160

Gentry RL (1970) Social behavior of the Steller sea lion. PhD. Dissertation. University of California, Santa Cruz, 113 pp

Gerke BL (2002) Spawning habitat characteristics of Pacific herring (*Clupea pallasii*) in PrinceWilliam Sound, Alaska. M.S. thesis. University of Alaska Fairbanks

Grass A (1973) Mew gulls and black turnstones feeding on herring eggs. Murrelet 54:38–39

Guillemette M, Ouellet J-F (2005) Temporary flightlessness in pre-laying common eiders *Somateria mollissima*: are females constrained by excessive wing-loading or by minimal flight muscle ratio? Ibis 147:293–300

Haegele CW (1993a) Seabird predation of Pacific herring, *Clupea pallasii*, spawn in British Columbia. Can Field-Nat 107:73–82

Haegele CW (1993b) Epibenthic invertebrate predation of Pacific herring, *Clupea pallasii*, spawn in British Columbia. Can Field-Nat 107:83–91

Haegele CW, Schweigert JF (1985) Distribution and characteristics of herring spawning grounds and description of spawning behaviour. Can J Fish Aquat Sci 42:39–55

Haegele CW, Schweigert JF (1989) Egg loss from Pacific herring spawns in Barkley Sound in 1988. Can. Manuscript Report Fish Aquat Sci 2037

Hamilton DJ, Barbeau MA, Diamond AW (2003) Shorebirds, mud snails, and *Corophium volutator* in the upper Bay of Fundy, Canada: predicting bird activity on intertidal mud flats. Can J Zool 81:1358–1366

Hay DE (1985) Reproductive biology of Pacific herring (*Clupea harengus*). Can J Fish Aquat Sci 42 (Suppl. 1):111–126

Hay DE, Kronlund AR (1987) Factors affecting the distribution, abundance, and measurement of Pacific herring (*Clupea harengus*) spawn. Can J Fish Aquat Sci 44:1181–1194

Hay DE, McCarter PB, Kronlund R, Roy C (1989) Spawning areas of British Columbia herring: a review, geographical analysis and classification. Volumes 1-VI. Can. Manuscript Report Fish Aquat Sci 2019

Hay DE, Toresen RR, Stephenson R, Thompson M, Claytor R, Funk F, Ivshina E, Jakobsson J, Kobayashi T, McQuinn I, Melvin G, Molloy J, Naumenko N, Oda KT, Parmanne R, Power M, Radchenko V, Schweigert J, Simmonds J, Sjöstrand B, Stevenson DK, Tanasichuk R, Tang R, Q, Watters DL, Wheeler J (2001) Taking stock: an inventory and review of world herring stocks in 2000. In: Funk F, Blackburn J, Day DH, Paul AJ, Stephenson R, Torresen R, Witherell D (eds) Herring expectation for a new millenium. Proceedings of the herring symposium 2000. Anchorage AK, pp 381–454

Heard WR (1991) Life history of pink salmon (*Oncorhynchus gorbuscha*). In: Groot C, Margolis L (eds) Pacific salmon life histories. University of British Columbia Press, Vancouver, BC, pp 119–230

Henderson RJ, Almatar SM (1989) Seasonal changes in the lipid composition of herring (*Clupea harengus*) in relation to gonad maturation. J Mar Biol Assoc U.K. 69:323–334

Heyman WD, Graham RT, Kjerfve B, Johannes RE (2001) Whale sharks *Rhincodon typus* aggregate to feed on fish spawn in Belize. Mar Ecol-Prog Ser 215:275–282

Hicklin PW (1987) The migration of shorebirds in the Bay of Fundy. Wils Bull 99:540–570

Hicklin PW, Smith PC (1979) The diets of five species of migrant shorebirds in the Bay of Fundy. Proc Nova Scotia Inst Sci 29:483–488

Hicklin PW, Smith PC (1984) Selection of foraging sites and invertebrate prey by migrant semipalmated sandpipers, *Calidris pusilla* (Pallas) in Minas Basin, Bay of Fundy. Can J Zool 62:2201–2210

Hicklin PW, Linkletter LE, Peer DL (1980) Distribution and abundance of *Corophium volutator* (Pallas), *Macoma balthica* (L.) and *Heteromastus filiformis* (Clarapede) in the intertidal zone of Cumberland Basin and Shepody Bay, Bay of Fundy. Can Tech Rep Fish Aquat Sci 965:1–59

Hildebrant GV, Schwartz CC, Robins CT, Jacoby ME, Hanley TA, Arthur SM, Servheen C (1999) The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Can J Zool 77:132–138

Hose JE, McGurk MD, Marty GD, Hinton DE, Brown ED, Baker TT (1996) Sublethal effects of the *Exxon Valdez* oil spill on herring embryos and larvae: morphological, cytogenetic, and histopathological assessments, 1989–1991. Can J Fish Aquat Sci 53:2355–2365

Janzen DH (1976) Why bamboos wait so long to flower. Annu Rev Ecol Syst 7:347–391

Jehl JR Jr (1988) Biology of the eared grebe and Wilson's phalarope in the nonbreeding seasons: a study of adaptations to saline lakes. Stud Avian Biol 12:1–74

Jönsson KI (1997) Capital and income breeding as alternative tactics of resource use in reproduction. Oikos 78:57–66

Jurasz C, Jurasz V (1979) Feeding modes of the humpback whale, *Megaptera novaeangliae*, in southeast Alaska. Scientific Rep Whale Res Inst 31:69–83

Kålås JA, Heggberget TG, Bjørn PA, Reitan O (1993) Feeding behaviour and diet of goosanders (*Mergus merganser*) in relation to salmonid seaward migration. Aquat Living Resour 6:31–38

Klaassen M, Lindström A, Meltofte H, Piersma T (2001) Arctic waders are not capital breeders. Nature 413:794

Kvist A, Lindström A, Green M, Piersma T, Visser GH (2001) Carrying large fuel loads during sustained bird flight is cheaper than expected. Nature 413:730–732

Lack D (1966) Population studies of birds. Clarendon Press, Oxford

Lasker R (1985) What limits clupeoid production? Can J Fish Aquat Sci 42 s(Suppl. 1):31–38

Lillegård M, Engen S, Sæther B, Toresen R (2005) Harvesting strategies for Norwegian spring-spawning herring. Oikos 110:567–577

Loughlin TR, Perlov AS, Vlaadimirov VA (1992) Range-wide survey and estimation of total number of Steller sea lions in 1989. Mar Mammal Sci 8:220–239

Loughlin TR, Sterling JT, Merrick RL, Sease JL, York AE (2003) Diving behaviour of immature Steller sea lions (*Eumetopias jubatus*). Fish Bull 101:566–582

Lowry LF, Frost KJ, VerHoef JM, DeLong RA (2001) Movements of satellite tagged subadult and adult harbor seals in Prince William Sound, Alaska. Mar Mam Sci 17:835–861

Marston BH, Willson MF, Gende SM (2002) Predator aggregations at eulachon (*Thaleichthys pacificus*) spawning runs in southeast Alaska. Mar Ecol-Prog Ser 231:229–236

Matthews SL, Boates JS, Walde SJ (1992) Shorebird predation may cause discrete generations in an amphipod prey. Ecography 15:393–400

Maurer BA (1990) Extensions of optimal foraging theory for insectivorous birds: implications for community structure. Stud Avian Biol 13:455–461

McClelland BR, Young LS, Shea DS, McClelland PT, Allen HL, Spetttigue EB (1982) The bald eagle concentration in Glacier National Park, Montana: origin, growth, and variation in numbers. Living Bird 19:133–155

McGurk MD, Brown ED (1996) Egg-larval mortality of Pacific herring in Prince William Sound, after the *Exxon Valdez* oil spill. Can J Fish Aquat Sci 53:2243–2354

McLarney WO (1967) Intrastream movement, feeding habits, and structure of a population of coast range sculpin, *Cottus aleuticus*, in relation to eggs of the pink salmon, *Oncorhynchus gorbuscha*, in Alaska. PhD. dissertation, University of Michigan, Ann Arbor

Meijer T, Drent R (1999) Re-examination of the capital and income dichotomy in breeding birds. Ibis 141:399–414

Merrick RL, Loughlin TR (1997) Foraging behavior of adult female and young-of-the-year Steller sea lions in Alaskan waters. Can J Zool 75:776–786

Morrison RIG, Hobson KA (2004) Use of body stores in shorebirds after arrival on high-arctic breeding grounds. Auk 121:333–344

Moulton LL (1999) Review of Lynn Canal herring. MJM Research, 1012 Shoreland Drive, Lopez Island, WA

Munro JA, Clemens WA (1931) Water fowl in relation to the spawning of herring in British Columbia. Biol Board Canada Bull XVII:1–46

Murdoch MH, Bärlocher F, Laltoo ML (1986) Population dynamics and nutrition of *Corophium volutator* (Pallas) in the Cumberland Basin (Bay of Fundy). J Exp Mar Biol Ecol 103:235–249

Myers JP (1986) Sex and gluttony on Delaware Bay. Nat Hist 95:68–77

Newton I (1998) Population limitation in birds. Academic Press, San Diego

Norcross BL, Hose JE, Fransden M, Brown ED (1996) Distribution, abundance, morphological condition, and cytogenetic abnormalities of larval Pacific herring in Prince William Sound, Alaska following the *Exxon Valdez* oil spill. Can J Fish Aquat Sci 53:2376–2387

Norton DW, Senner SE, Gill RE Jr, Martin PD, Wright JM, Fukuyama AK (1990) Shorebirds and herring roe in Prince William Sound, Alaska. Am Birds 44:367–371

Odum WE, Odum EP, Odum HT (1995) Nature's pulsing paradigm. Estuaries 18:547–555

Olson JM, McNeil WJ (1967) Research on pink salmon at Little Port Walter, Alaska, 1934–1964. U. S. Fish and Wildlife Service Data Report 17, Washington DC

Ostfeld RS, Keesing F (2000) Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends Ecol Evol 15:232–237

Outram DN (1958) The magnitude of herring spawn losses due to bird predation on the west coast of Vancouver Island. Fish Res Board Canada, Progress Reports of the Pacific Coast Stations No. 111:9–13

Outram DN, Humphreys RD (1974) The Pacific herring in British Columbia waters. Circular 100, Fisheries and Marine Service, Pacific Biological Station, Nanaimo, B. C

Palsson WA (1984) Egg mortality upon natural and artificial substrata within Washington State spawning grounds of Pacific herring (*Clupea harengus*). M. S. thesis, University of Washington, Seattle. 191 pp

Paton DC (1986) Honeyeaters and their plants in south-eastern Australia. In: Ford HA, Paton DC (eds) The dynamic partnership: Birds and plants in southern Australia. Woolman, Government Printer, South Australia, pp 9–19

Paul AJ, Paul JM (1999) Energy contents of whole body, ovaries, and ova from pre-spawning Pacific herring. Alaska Fishery Res Bull 6(1):29–34

Paul AJ, Paul JM, Brown ED (1996) Ovarian energy content of Pacific herring from Prince William Sound, Alaska. Alaska Fishery Res Bull 3(2):103–111

Pearce-Higgins JW, Yalden DW (2004) Habitat selection, diet, arthropod availability and growth of a moorland wader: the ecology of European golden plover *Pluvialis apricaria* chicks. Ibis 146:335–346

Peer DL, Linkletter LE, Hicklin PW (1986) Life history and reproductive biology of *Corophium volutator* (Crustacea: Amphipoda) and the influence of shorebird predation on population structure in Chignecto Bay, Bay of Fundy, Canada. Netherlands J Sea Res 20:359–373

Pfister C, Kasprzyk MJ, Harrington BA (1998) Body-fat levels and annual return in migrating semipalmated sandpipers. Auk 115:904–915

Piatt JF (1990) The aggregative response of common murres and Atlantic puffins to schools of capelin. Stud Avian Biol 14:36–51

Pierotti R (1988) Associations between marine birds and mammals in the northwest Atlantic Ocean. In: Seabirds and other marine vertebrates: competition, predation, and other interactions. Columbia University Press, New York, pp 31–58

Piersma T (1998) Phenotypic flexibility during migration: optimization of organ size contingent on the risks and rewards of fueling and flight? J Avian Biol 29:511–520

Pitcher KW (1980) Food of the harbor seal (*Phoca vitulina richardsi*) in the Gulf of Alaska. Fishery Bull 78:544–549

Pitcher KW (1981) Prey of the Steller sea lion, *Eumetopias jubatus*, in the Gulf of Alaska. Fishery Bull 79(3):467–472

Raum-Suryan KL, Rehberg MJ, Pendleton GW, Pitcher KW, Gelatt TG (2004) Dispersal, movement patterns, and haulout use of pup and juvenile Steller sea lions (*Eumetopias jubatus*) in Alaska. Mar Mamm Sci 20:823–850

Restani M, Harmata AR, Madden EM (2000) Numerical and functional responses of migrant bald eagles exploiting a seasonally concentrated food source. Condor 102:561–568

Rodway MS, Cooke F (2001) Effect of food availability on arrival and departure decisions of harlequin ducks at diurnal feeding grounds. Condor 103:870–874

Rodway MS, Cooke F (2002) Use of fecal analysis to determine seasonal changes in the diet of wintering harlequin ducks at a herring spawning site. J Field Ornith 73:363–371

Rodway MS, Regehr HM, Ashley J, Clarkson PV, Goudie RI, Hay DE, Smith CM, Wright KG (2003) Aggregative response of harlequin ducks to herring spawning in the Strait of Georgia, British Columbia. Can J Zool 81:1–11

Rooper CN (1996) Physical and biological factors affecting Pacific herring egg loss in Prince William Sound, Alaska. M.S. thesis, University of Alaska-Fairbanks, 195 pp

Rosen DAS, Trites AW (2000) Digestive efficiency and dry-matter digestibility in Steller sea lions fed herring, pollock, squid, and salmon. Can J Zool 78:234–239

Rosen DAS, Trites AW (2002) Cost of transport in Steller sea lions, *Eumetopias jubatus*. Mar Mam Sci 18:513–524

Rounsefell GA, Dahlgren EH (1935) Races of herring, *Clupea pallasii*, in southeastern Alaska. Bull Bureau Fisher 58:119–141

Sandegreen FE (1970) Breeding and maternal behavior of the Steller sea lion (*Eumetopias jubatus*) in Alaska. M.S. thesis, University of Alaska Fairbanks, 138 pp

Sigler MF, Womble, J.N, Vollenweider JJ (2004) Availability to Steller sea lions (*Eumetopias jubatus*) of a seasonal prey resource: a prespawning aggregation of eulachon (*Thaleichthys pacificus*). Can J Fish Aquat Sci 61:1475–1484

Similä T, Ugarte F (1993) Surface and underwater observations of cooperatively feeding killer whales in northern Norway. Can J Zool 71:1494–1499

Similä T, Holst JC, Christensen I (1996) Occurrence and diet of killer whales in northern Norway: seasonal patterns relative to the distribution and abundance of Norwegian spring-spawning herring. Can J Fish Aquat Sci 53:769–779

Smith RJ (2003) Resources and arrival of landbird migrants at northerly breeding grounds: linking en route with breeding season events. PhD thesis, University of Southern Mississippi

Soto KH, Trites AW, Arias-Schreiber M (2004) The effects of prey availability on pup mortality and the timing of birth of South American sea lions (*Otaria flavescens*) in Peru). J Zool Lond 264:419–428

Soto KH, Trites AW, Arias-Schreiber M (2006) Changes in diet and maternal attendance of South American sea lions indicate changes in the marine environment and prey abundance. Mar Ecol Prog Ser 312:277–290

Stephens DW (1990) Foraging theory: up, down, and sideways. Stud Avian Biol 13:444–454

Straley JM (1990) Fall and winter occurrence of humpback whales (*Megaptera novaeangliae*) in southeastern Alaska. Rep Int Whaling Commission, Special Issue 12:319–323

Sullivan TM, Butler RW, Boyd WS (2002) Seasonal distribution of waterbirds in relation to spawning Pacific herring, *Clupea pallasii*, in the Strait of Georgia, British Columbia. Can Field-Nat 116:366–370

Taylor SG, Lum JL (2005) Auke Creek Weir 2004. Annual report, operations, fish counts, and historical summaries. National Marine Fisheries Service, Auke Bay Laboratory, 22305 Glacier Hwy, Juneau AK 99801. Unpublished report 26 pp

Thomas GL, Thorne RE (2001) Night-time predation by Steller sea lions. Nature 411:1013

Thompson JN, Willson MF (1979) Evolution of temperate fruit/bird interactions: phenological strategies. Evolution 33:973–982

Thorne RE (2005) Monitoring Pacific herring abundance with combined acoustic and optical technologies. Proceedings Oceans 05. Washington, D.C. Sept. 20–23

Trillmich F, Ono KA (1991) Pinnipeds and El Niño: responses to environmental stress. Springer-Verlag, Berlin

Tsipoura N, Burger J (1999) Shorebird diet during spring migration stopover on Delaware Bay. Condor 101:635–644

Van Opzeeland IC, Corkeron PJ, Leyssen T, Similiä T, Van Parijs SM (2005) Acoustic behaviour of Norwegian killer whales, *Orcinus orca*, during carousel and seiner foraging on spring-spawning herring. Aquat Mammals 31:110–119

VerHoef JM, Frost KJ (2003) Bayesian hierarchical model for monitoring harbor seal changes in Prince William Sound, Alaska. Environ Ecol Stat 10:201–209

Vermeer K (1981) Food and populations of surf scoters in British Columbia. Wildfowl 32:107–116

Vermeer K (1983) Marine bird populations in the Strait of Georgia: comparison with the west coast of Vancouver Island. Can Tech Rep Hydrography Ocean Sci 19:1–18

Vermeer K (1992) The diet of birds as a tool for monitoring the biological environment. Occas. Paper, Can Wildlife Serv 75:41–50

Vermeer K, Bourne N (1983) The white-winged scoter diet in British Columbia waters: resource partitioning with other scoters. In: Nettleship DN, Sanger GA, Springer PF (eds) Marine birds: their feeding ecology and commercial fishing relationships, Can. Wildlife Serv. Report for the Pacific Seabird Group, pp. 30–38

Vermeer K, Morgan KH (1992) Marine bird populations and habitat use in a fjord on the west coast of Vancouver Island. In Vermeer K, Butler RW and Morgan KH (eds) The ecology, status, and conservation of marine and shoreline birds on the west coast of Vancouver Island. Occas. Paper No. 75, Can. Wildlife Ser, pp 86–95

Vermeer, K., Bentley M, Morgan KH, Smith GEJ (1997) Association of feeding flocks of brant and sea ducks with herring spawn at Skidegate Inlet. In: Vermeer K, Morgan KH (eds) The ecology, status, and conservation of marine and shoreline birds of the Queen Charlotte Islands. Occas Paper Can Wildlife Serv. 93:102–107

Vermeer K, Morgan KH, Dorst A, Whittington B (1992) Bird populations of estuaries on the southwest coast of Vancouver Island. In: Vermeer K, Butler RW, Morgan KH (eds) The ecology, status, and conservation of marine and shoreline birds in the west coast of Vancouver Island. Occas Pap Can. Wildlife Serv 75:97–108

Ware DM (1985) Life history characteristics, reproductive value, and resilience of Pacific herring (*Clupea harengus*). Can J Fish Aquat Sci 42 (Suppl. 1):127–137

Weidensaul S (1999) Living on the wind. North Point Press, New York, 340 pp

Wespestad VG, Barton LH (1979) Distribution, migration, and status of Pacific herring. Nat. Mar. Fish. Serv., Northwest and Alaska Fisheries Center, Seattle WA. pp 509–525

Willson MF, Halupka KC (1995) Anadromous fish as ''keystone'' resources in vertebrate communities. Cons Biol 9:489–497

Willson MF, Marston BH (2002) Fishing success of gulls at a Southeast Alaska smelt run. J Field Ornith 73:91–96

Willson MF, Gende SM (2004) Seed dispersal by brown bears, *Ursus arctos*, in southeastern Alaska. Can Field-Nat 118:499–503

Willson MF, Gende SM, Marston BH (1998) Fishes and the forest. BioScience 48:455–462

Wilson WH Jr (1990) Relationship between prey abundance and foraging site selection by semipalmated sandpipers on a Bay of Fundy mudflat. J Field Ornith 61:9–19

Womble JN, Sigler MF (in press) Seasonal availability of abundant, energy-rich prey influences the abundance and diet of a marine predator, the Steller sea lion *Eumetopias jubatus*. Mar Ecol-Prog Ser

Womble JN, Willson MF, Sigler MF, Kelly BP, VanBlaricom GR (2005) Distribution of Steller sea lions (*Eumetopias jubatus*) in relation to spring-spawning prey species in Southeastern Alaska. Mar Ecol-Prog Ser 294:271–282

Wood CC (1987) Predation of juvenile Pacific Salmon by the Common Merganser (*Mergus merganser*) on eastern Vancouver Island. I: predation during the seaward migration. Can J Fish Aquat Sci 44:941–949

Yang LH (2004) Periodical cicadas as resource pulses in North American forests. Science 306:1565–1567