Humpback Whale Predation and the Case for Top-Down Control of Local Herring Populations in the Gulf of Alaska

by
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During late winter in Lynn Canal Steller sea lions closely coordinate foraging dives with a humpback whale to capitalize on minor disruptions to the herring school caused by whales. Photo by John Moran.

Control over the production of highly fecund species such as Pacific herring (*Clupea pallasii*) has been attributed historically to bottom-up effects such as ocean conditions or food availability. In contrast, top-down control exists when predation limits population production. Recent observations of humpback whales (*Megaptera novaeangliae)* foraging on depressed herring populations suggests top-down control of herring may be underappreciated. Pacific herring populations are depressed in several locations in Alaska, and humpback whale populations are increasing. A 2004-06 census estimated the North Pacific humpback whale population at 18,000 to 20,000 and concluded that the population of whales wintering in Hawaiian waters (one half of the North Pacific population) is doubling approximately every 15 years. Humpback whales could potentially be a significant source of mortality on herring populations because they are large homeotherms that often consume herring, and they display a remarkable fidelity to their feeding grounds. If whales repeatedly return to locations to forage with increasing numbers, then production of their prey may become constrained. Anecdotal evidence of humpback whales foraging in locations where herring populations are depressed led to the hypothesis that humpback whale predation impedes the recovery of depressed herring populations, even when the commercial herring fisheries have been closed for decades.

It is important to understand the effect of humpback whales on herring because both species are conspicuous elements in the Gulf of Alaska ecosystem. Herring are ubiquitously distributed and play a key role in the ecosystem by making the energy bound in primary consumers available to apex predators. Humpback whales are voracious predators. A humpback whale weighs around 30 metric tons (t) and requires the equivalent of about 1,100 herring per day to meet its average daily metabolic cost. However, while it is evident that whales depend on herring to some degree, the impact of this dependence on herring is unknown.

If we are to evolve towards ecosystem-based management, we will need to begin quantifying the benefits whales gain from herring and the costs of whale predation to herring. Understanding the relationship between herring and humpback whales is a goal of the Auke Bay Laboratories' (ABL) Nutritional Ecology Lab. Beginning in 2001, we began documenting seasonal changes in the energy content of herring as winter progresses in the local population in Lynn Canal, a fjord adjacent to the ABL facility. Winter is an overlooked time of year critical to the survival and production of many marine species, and our location near a significant herring biomass facilitates our ability to understand these processes. In 2007, our studies expanded when we began comparing the effects of whales on three different herring populations. Our approach was to estimate the biomass of herring consumed by whales in each location and observe herring behavior in response to whale predation.

Herring and whale studies in the Gulf of Alaska

The location of greatest concern for the impacts of whale predation on herring stocks has been Prince William Sound. In 1993 the Prince William Sound herring stock, which had been fished commercially for decades, suddenly collapsed due to an

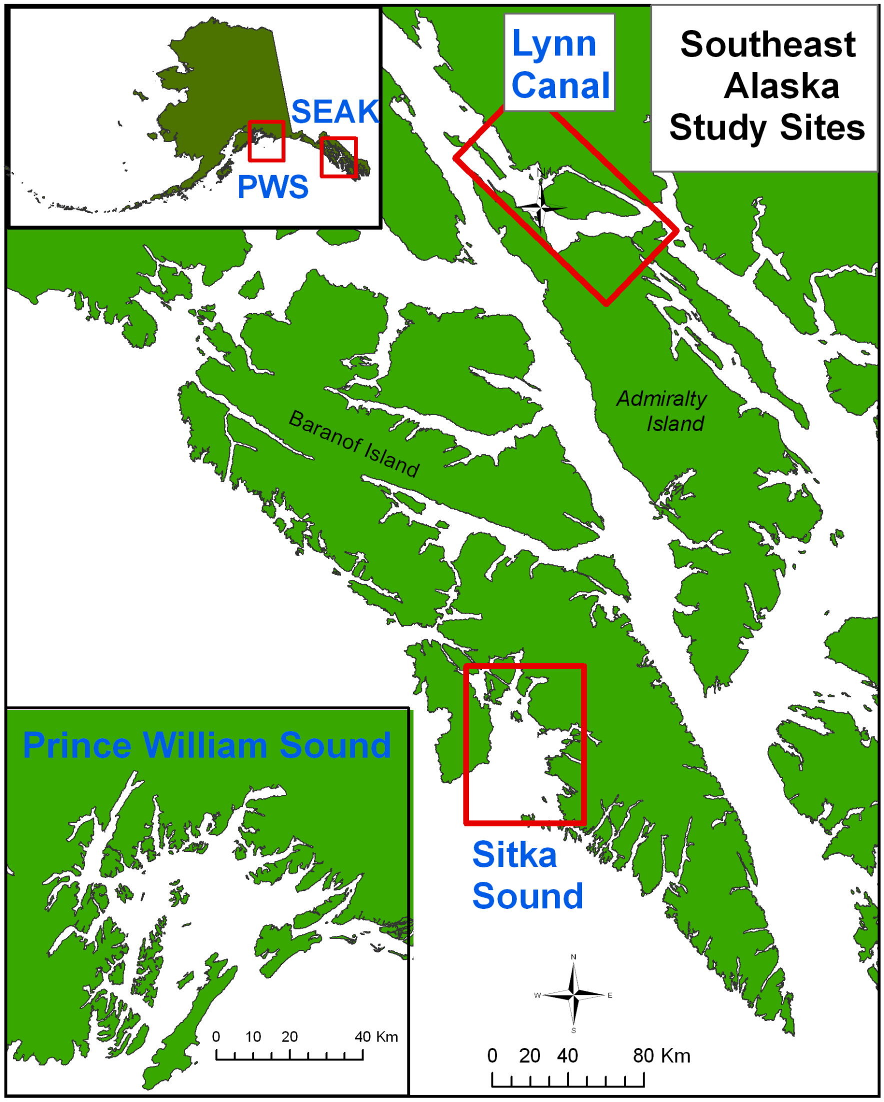

Figure 1. Location of the Prince William Sound (PWS), Lynn Canal, and Sitka Sound study areas in Southeast Alaska (SEAK).

Figure 2. The unique patterns on the flukes of humpback whales identify individuals allowing the use of mark-recapture models to estimate whale abundance. Photo by John Moran.

outbreak of viral hemorrhagic septicemia. The fishery was closed and has essentially remained so to this day. Whale predation has been cited as one possible explanation for the failed recovery. This hypothesis derived from reports of humpback whales foraging in Prince William Sound all winter in locations where herring were known to congregate.

We began examining this question in detail in Prince William Sound in fall 2007 and included Sitka Sound and Lynn Canal (Fig. 1) as reference sites. We included Sitka Sound because it supports a commercially viable herring population with a total biomass currently near 85,000 t. Whales have been observed foraging on herring in Sitka Sound since the early 1980s. We included Lynn Canal because the herring population has failed to support a commercial fishery after being closed to commercial fishing for more than a quarter of a century. Though the cause for the depression of the Lynn Canal population is unknown, humpback whale populations there have been increasing. We focused on these three areas in winter, a time when herring congregate in each location. These concentrations of herring made it easier for us to observe whale foraging behaviors.

While there were reports of whales foraging in winter in Alaskan waters it was unlikely that whales foraged on herring all winter. Humpback whales make transoceanic migrations from their feeding grounds in the North Pacific to calving grounds near Hawaii in winter. It is known that whales stagger their departure from their feeding grounds, suggesting they also stagger their return. This could create the impression that whales were present throughout the entire winter. Only by identifying individual whales and enumerating them would it be possible to establish the extent of winter foraging. Individual identification of humpback whales is done by photographing and cataloging the unique markings on the undersides of their flukes (Fig. 2).

We used these individual markings in mark-recapture studies to estimate the number of whales present throughout the winter in each of the three locations. We developed monthly estimates of whale abundance for the winters of 2007-08 and 2008-09. We concurrently identified the types of prey consumed by whales through fatty acid analysis, direct observation, and acoustic observation (Fig. 3). Combining our observations of whale abundance and the proportion of whales consuming herring with bioenergetic models, we estimated the biomass of herring consumed by whales over winter in each location. We compared these estimates to the estimated total biomass of herring present after spawning for the three populations to determine what proportion of the total biomass the whales were likely consuming. The herring population numbers were obtained from age-structured stock assessments for Sitka and Prince William Sounds and estimates of spawning stock biomass for Lynn Canal. All of these herring estimates were produced by the Alaska Department of Fish and Game (ADF&G).

Our previous work with Lynn Canal herring indicated comparisons between whale consumption and spawning stock biomass would overestimate the whale impact because there are significantly more herring present in winter than are observed during spawning. Consequently, we conducted monthly acoustic surveys in Lynn Canal during winter to estimate herring abundance and estimate the potential predation rate on a monthly basis. One of the benefits of simultaneously conducting the acoustic and whale abundance surveys was that we could examine the effects of whales on herring by mapping the distribution of whales and herring and comparing the abundance of whales with the depth and location of herring schools in the water column.

Estimates of whale predation on wintering herring

Humpback whales consumed herring at each location, but their direct impact on herring varied considerably among locations. All three whale populations declined seasonally at the end of winter, but the trends in seasonal abundance and the effort they expended on foraging for herring differed among locations. Seasonal trends in whale abundance were similar between Lynn Canal and Sitka Sound peaking earlier in the fall. But when whales were abundant in Sitka Sound they foraged on krill, while Lynn Canal whales foraged on herring (Table 1). In Prince William Sound whale numbers remained high into mid-winter (Fig. 4), and they foraged primarily on herring throughout the winter. The timing of peak whale abundance in all locations corresponded to the time when herring have their highest energy content.

In Sitka Sound, the lack of feeding in the early fall on herring was directly related to the absence of herring and abundance of krill. In winter, the number of whales observed eating herring increased after herring arrived in Sitka Sound. However, as winter progressed herring began staging for spawning at the same time whales departed for their breeding grounds. Therefore, even though herring were abundant, there were few whales present and consumption rates were low.

In Lynn Canal we observed the opposite pattern: whales consumed herring in October and November when whales were abundant and herring densities were just beginning to increase. However, by mid-December when herring density was very high we could no longer determine what whales were eating and their numbers were in steep decline.

In contrast to Sitka Sound and Lynn Canal, whales in Prince William Sound almost always consumed herring and stayed until January. Krill appeared to be relatively rare in the area.

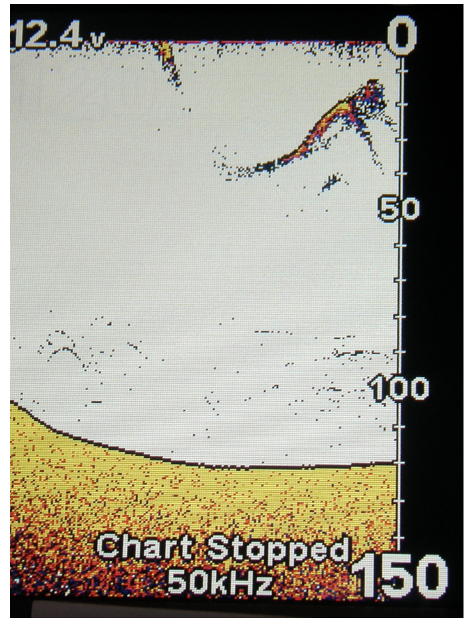

Figure 3. In this echogram recorded at 50 kHz a humpback whale can be seen attacking a small herring school near the surface. Depth intervals are displayed in meters. In January, when this echogram was recorded, herring schools were dispersed by whales and scattered throughout the water column in Prince William Sound.

The differences in whale abundance and apparent preference for herring led to very different estimates of herring consumption in each location (Table 2). In Sitka Sound, whales consumed an estimated 800-1,000 t of herring in late winter. However the estimated biomass of herring the previous spring was about 100,000 t, so whale consumption amounted to less than 1% of the herring biomass. In contrast, whales in Prince William Sound consumed 2,600–4,300 t of herring over winter, which translated to 20%-25% of the total herring biomass. Lynn Canal whales ate 500-700 t of herring over winter or almost all of the local spawning stock. But, recall herring abundance in Lynn Canal during winter exceeds the spawning stock biomass. In November, whales consumed 1%-2% of the biomass present. After November consumption dropped to less than 1% because whales departed and herring continued to arrive.

It is important to put the impact of the humpback whales on the Prince William Sound herring into perspective. The pro-

Table 1. The proportion of whales observed foraging on herring during monthly surveys in Lynn Canal, Prince William and Sitka Sounds over the winters of 2007-08 and 2008-09.

Period	Lynn Canal	Prince William Sound	Sitka Sound
Sep. 15 – Oct. 15	1.0	0.86	0
Oct. 16 – Nov. 15	1.0	0.90	0.17
Nov. 16 – Dec. 15	0.63	0.94	0.58
Dec. 16 – Jan. 15	0	1.0	0.57
Jan. 16 – Feb. 15	0	1.0	1.0
Feb. 15 – Mar. 15	0	1.0	1.0

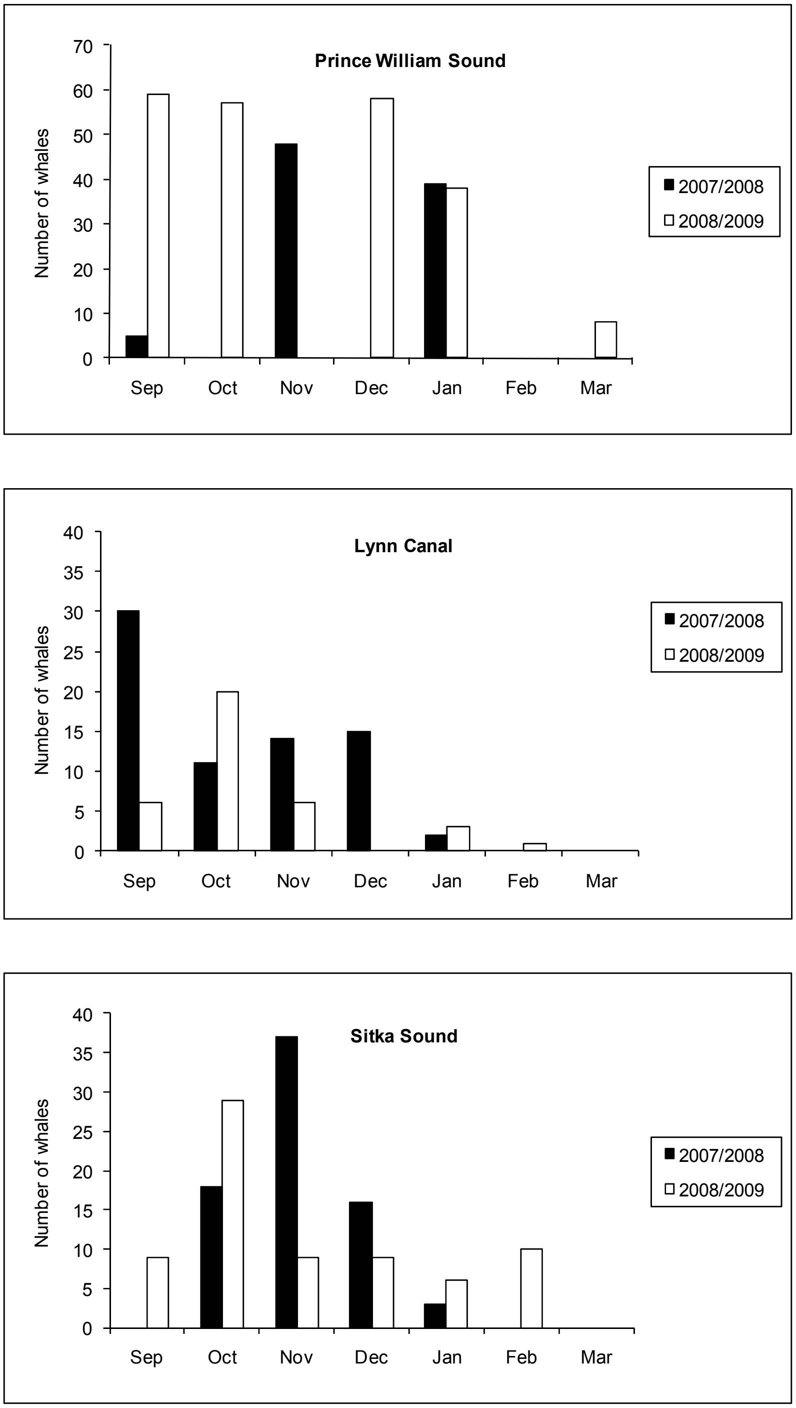

Figure 4. The number of individual humpback whales identified each month from fluke photographs in Prince William Sound, Lynn Canal, and Sitka Sound during the fall and winter months for 2007-08 and 2008-09. These values were expanded in the bioenergetic model to account for mark-recapture estimates of the total number of whales present.

portion of herring consumed is approximately equal to the number that would be removed if a commercial fishery were to take place. The guideline harvest level for herring in Prince William Sound varies between 15% and 20% of the total biomass, depending on the size of that biomass. The effect of the whales is therefore consistent with that of a sustainable commercial fishery, but the whales can remove herring even if the stock biomass is less than 22,000 t, the statutory threshold for commercial fishing. Another way to look at the impact is to compare the biomass consumed with the estimated biomass lost to natural mortality according to the age-structured stock assessments. These latter estimates range between 1,800 and 5,500 t lost per winter, suggesting whales might well account for nearly all of the natural mortality. Consequently, the true impact of humpback whales on Prince William Sound herring depends on the proportion of natural mortality that can be ascribed to whale predation.

Response of herring to whale predation

An important result of our combined whale and herring acoustic surveys in Lynn Canal was that we were able to describe the behavior of wintering herring and determine how humpback whales influence that behavior. Herring display a characteristic set of behaviors in winter, but we do not yet fully understand the impact of these behaviors on herring productivity. In the course of our surveys we were able to establish a correlation between the abundance of whales and herring schooling behavior, which suggests whales exert indirect effects on herring behavior that make them susceptible to predation by other surface-oriented predators.

Herring wintering behavior includes aggregating in predictable locations

During the fall and winter months Pacific herring exhibit a behavioral change; switching from smaller, dispersed, mobile, foraging schools found throughout the water column to forming large, dense shoals in the deeper trenches of bays and fjords where little feeding takes place. More than 30,000 t of herring move into Lynn Canal between October and March, where there are only 1,000 t during the rest of the year. The arriving herring demonstrate three important characteristics of wintering herring: 1) aggregation in a predictable location, 2) reduced foraging, and 3) formation of massive schools at depth. In Lynn Canal these schools can be more than 20 km long and 30 m thick. Similar behavior occurs in Atlantic herring. For example, over 10 million t of the Norwegian spring-spawning herring, the entire population, winter in only two fjords on the northwest coast of Norway.

Of these three characteristics, aggregation in a predictable location is the least understood. Reduced foraging is likely due to diminished food supplies in winter, and formation of massive schools at depth probably is an effort to avoid predation from surface-oriented predators. Site selection is less clear, but likely involves efforts to minimize predation from predaceous fish and minimize energy costs. As herring move into nearshore fjords in winter, piscivorous fish, such as halibut, arrowtooth flounder, sablefish, gadids, and rockfish move offshore. At the same time, herring begin maturing, an energetically demanding process. For example, Lynn Canal herring lose about 44% of their body mass and about 58% of their energy content over winter while the energy content of their gonads increases by approximately 600%. Cold water temperatures and slow water currents in deep trenches occupied by herring may reduce their metabolic costs and provide an energetic refuge. The formation of large schools in these refugia may offer some additional energetic advantage by increasing swimming efficiency.

While movement into nearshore fjords may protect herring from piscivorous fish, it places them in close proximity to a variety of surface-oriented predators. By forming massive schools at depth, individual herring can reduce their exposure to pinnipeds and diving seabirds. However, formation of such schools at depth may serve to increase their vulnerability to humpback whales. Humpback whales routinely forage at depths consistent with the location of these schools and can ingest hundreds of fish at a time. Hence there is likely a trade-off between formation of deepwater schools and the risk of predation by humpback whales.

Whales delay the formation of large deep schools

During early winter when whales were abundant, herring were distributed over a relatively large spatial area (Fig. 5) and located higher in the water column (Fig. 6). After the whales departed, the herring coalesced into one large school and moved deeper in the water. This correlation suggests a functional relationship in which whale foraging delays formation of the large deep school. Fin whales have been shown to disrupt schools of migrating herring in Norway, and that seems to be the case here with humpback whales. Schooling is thought to be adaptive for individuals because joining with a large number of fish reduces the probability of being predated, so the benefit increases with school size. While this may be true when predators consume a single fish at a time, humpback whales can ingest up to 60,000 liters of water and presumably hundreds of herring in one swallow. Certainly a large school in a predictable location would be relatively easy for a whale to locate, while smaller dispersed schools would be more difficult. Formation of large schools may reduce whale searching costs and makes herring a more attractive prey. Alternatively, the repeated disruption of the large school by foraging whales may simply prevent the school from coalescing. Sorting out these alternatives is important because the presence of small herring schools in winter might be used to index predation intensity.

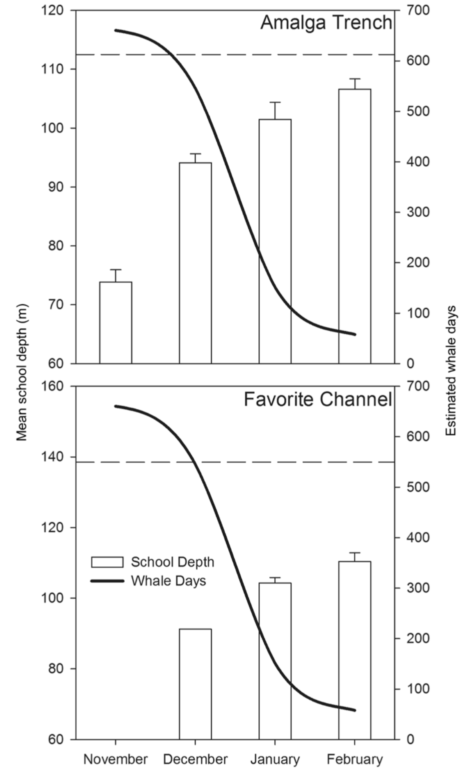

Figure 5. Monthly vertical distribution of Pacific herring schools in two locations in Lynn Canal and the estimated whale days for all of Lynn Canal during 2007-08 and 2008-09 winter months (Nov-Feb). Broken line on each plot represents mean water depth where herring schools were observed in both substrata. Error bars represent standard error.

Regardless of how the whales delay formation of large schools, the location of the schools higher in the water column increases herring vulnerability to other predators. The large deepwater school formed in late winter is found at depths below 100 m. Humpback whales routinely forage at that depth. But the metabolic returns and risk of predation favor dives to shallower water for Steller sea lions and diving seabirds. In fall and early winter when the deepwater school had not coalesced, herring occupied depths between 50 and 100 m, well within sea lion and seabird diving range. Coincidently, we have observed a 64% decrease in the average mass of herring in sea lion scats between December and February in Lynn Canal even though her-

Table 2. Estimates of herring biomass removed from Lynn Canal, Sitka and Prince William Sounds. Consumption estimates are based on a bioenergetic model incorporating whale abundance, the proportion consuming herring and an allometric relationship between whale size and average daily metabolic rate. Total herring biomass is the estimated biomass of herring present in the spring prior to the winter in question as determined from stock assessments conducted by the Alaska Department of Fish and Game. Relative to spawning biomass, estimates of herring consumed in Lynn Canal very large in 2007-08 and exceeds the spawning stock biomass in 2008-09. As Lynn Canal is an overwintering location for herring, biomass increases significantly during the winter when consumption estimates are less than 2%.

Location	Winter	Herring consumed (t)	Total herring biomass[1] (t)	Percentage of total biomass consumed
Lynn Canal	2007-08	732	1,461	50%
	2008-09	501	499	100%
Sitka Sound	2007-08	1,018	101,209	1%
	2008-09	813	108,192	1%
Prince William Sound	2007-08	2,639	9,650	27%
	2008-09	4,388	20,737	21%

[1] Alaska Department of Fish and Game

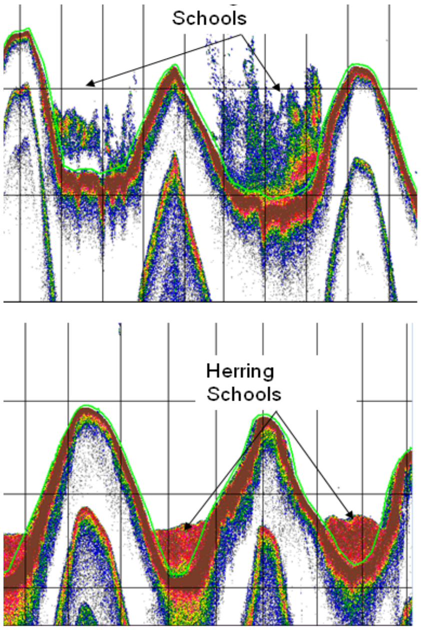

Figure 6. Example echograms of herring distributions observed at 38 kHz during November (A) and February (B) in Lynn Canal, Alaska. Depth intervals are displayed at 50-m increments, and horizontal cells are separated by 0.1 nmi. Herring schools are clearly more dispersed and shallower in November, whereas herring form dense schools in the deep trenches during February. The green thin line represents the seafloor.

ring were the most frequently occurring prey in both collections. Surface-oriented predators also benefit from whale foraging because whales are relatively sloppy predators, leaving many stunned fish near the surface (Fig. 7).

If whales interfere with the formation of deepwater herring schools in Lynn Canal, then we would expect an even greater delay among herring in Prince William Sound where whale predation was sustained over a longer time period. Acoustic surveys of Prince William Sound conducted by the ADF&G did find large deepwater schools in November. However, these schools were near the spawning grounds. In Sawmill Bay where there was heavy whale predation on herring, herring were dispersed throughout the water column. If herring need to overwinter in areas that minimize their metabolic demand and formation of deepwater schools provide some energetic benefit, then whale predation in Prince William Sound may be influencing the energetics of herring reproduction. We plan to test this hypothesis with samples of adult herring we collected in 2007-08 and 2008-09. In another study, we have observed accelerated energy loss among overwintering juveniles from Prince William Sound relative to those in Sitka Sound or Lynn Canal. Humpback whale foraging may account for this discrepancy, but we do not know the extent to which whales forage on juvenile herring.

Conclusion

It is clear from our data that whales are affected by herring and herring are affected by whales. A significant number of whales rely on herring as prey and remove relatively large amounts of herring from the ecosystem. In turn, the amount of herring whales remove from some populations can represent a significant source of mortality, as in Prince William Sound. However, the extent to which whale-induced mortality exceeds current estimates of natural mortality, if at all, is unknown. We have also shown that whales can increase mortality by making herring more accessible to other predators. It is unlikely that these predators impact herring populations on the same scale as whales. But they directly benefit from the relationship between whales and wintering herring as a result in increased access to energy-rich prey during a critical time of year. The degree to which these species benefit from this prey indicates the importance of this function whales provide. We have little appreciation for the ecological role humpback whales play because we have yet to witness a marine ecosystem with whales at known pre-exploitation population levels. However, the ecological literature is replete with examples of the far reaching and unanticipated effects as apex predators re-enter ecosystems. Our work has revealed that as humpback whales impact one resource they improve conditions for others. While the significance of these effects are not currently understood, their valuation is likely to change as humpback whales become more abundant. Currently the Exxon Valdez Oil Spill Trustee Council is contemplating several restoration options for Prince William Sound herring. Predation by humpback whales presents a daunting obstacle to these efforts. Moreover, enhancing bottom-up processes may have little effect on herring production if the top-down effects exerted by whales continue to be a dominating force.

Figure 7. Gulls feeding on hundreds of stunned herring brought to the surface by a humpback whale. By disrupting herring aggregations at depth, whales make herring available to other air breathing predators with limited diving abilities. Photo by John Moran.