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acoustic assessment of trophic dominance in a marine ecosystem

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Abstract: The results from sixteen years of acoustic surveys suggest that Prince William Sound (PWS), Alaska, functions as a wasp-waist ecosystem. The planktivorous fishes that dominate the wasp waist are Pacific herring (10-100 thousand tons) and walleye pollock (10-50 thousand tons). The dominant macrozooplankton prey are the large-bodied copepods (Neocalanus spps., 50 thousand tons), and comparable sized abundances of pteropods, and euphausids, which are also the primary forage of juvenile fishes such as pink salmon. The herring and pollock consume the bulk of the spring macrozooplankton, so they are major competitors as well as predators of juvenile fishes. Their individual abundances also affect the composition and production of the top piscivores in the ecosystem. The near-shore and near-surface distribution of herring in the winter makes them the most available forage for surface-oriented marine mammal and seabird predators. In contrast, the deep, off-shore distribution of pollock favours large benthic predators, such as arrowtooth flounder and large sharks. The acoustic surveys demonstrated that high abundance of copepods, pteropods, and euphausids distract the wasp-waist fishes in the spring, creating possible loopholes in predation for nearshore juvenile fishes like pink salmon, allowing them to have a successful recruitment year. An additional outcome of the long-term database on Pacific herring was the discovery of linkages between the 1989 "Exxon Valdez" oil spill and a subsequent collapse of the herring along with associated predators.

1 Introduction

In 1991-93, GLOBEC planning documents were used to design an ecosystem program in Prince William Sound (PWS), Alaska [1,2,3]. This effort evolved into several programs, including the Sound Ecosystem Assessment (SEA) program [4,5]. Neither the SEA program nor the east and west coast GLOBEC programs were particularly successful at implementing primary synoptic sampling with acoustical-optical technologies. However, the SEA program did have the advantage of working in a much smaller, semi-contained ecosystem, which forced sampling into a smaller space. Since much of the sampling was conducted by a local institution (Prince William Sound Science Center) with local charter vessels, the sampling frequency in time was more continuous, especially in the winter months where there was a void of scientific observations. After a decade of quantitative monitoring built around acoustical-optical assessment techniques, including the five-year SEA program, we documented six major biomasses. Three were pelagic/semi-pelagic, dominantly planktivorous fishes: the Pacific herring (Clupea pallasi), walleye pollock (Theragra chalcogramma) and the transient pink salmon (Oncorhynchus gorbuscha), which only dominated the biomass when it returned to the Sound to spawn in the summer. The other three were macrozooplankton groups: pteropods, euphausids and the large-bodied copepods of the genus Neocalanus, which dominate the spring zooplankton biomass.

At the start of our ecosystem research the traditional concepts for biological forcing in marine food webs were top-down and bottom-up processes. However, during the SEA program a more contemporary concept of wasp-waist or middle-out forcing was developed [6]. Arctic, subarctic, upwelling and temperate food webs that are dominated by one or two planktivorous fishes, such as sardine and anchovy, were being classified as wasp-waist ecosystems with middle-out forcing [7]. In this paper we present evidence that the middle-out, or wasp-waist mechanism is working in the PWS ecosystem. We show that a focus on the dominant middle-trophic level biomasses yields quantitative information on ecosystem function that is fundamental to understanding long-term population, food web and ecosystem change.

2 Methods

We conducted the first acoustic survey of Pacific herring in 1993 after fishers were unable to locate fishable concentrations of herring despite a preseason prediction from an age-structured assessment (ASA) model of an extremely large population. Subsequently at least one annual survey has been conducted each year for 16 consecutive years. Survey procedures have been previously detailed [8,9]. Key features are the use of calibrated scientific echosounders, scanning sonars and aerial surveillance along with infrared optics, underwater video, purse seine, midwater trawl and plankton net sampling, in an adaptive, repeated, multi-stage survey design. Beginning in 2000, the surveys incorporated census of the marine mammals and seabirds near the herring aggregations [8,10].

The first walleye pollock survey was conducted in 1995. In contrast with herring, the impetus for this first acoustic survey of walleye pollock was the discovery by fishers of large aggregations of pollock that were not consistent with the ASA estimates of biomass used to set harvest quotas (Underlying our experience is the concept that industry and not government is the entity that forces real change in management practices and the status quo). Subsequent surveys were conducted in 1997, 1998 and 2000 to 2003. Survey methodology has been previously detailed [11].

We began a study of spring zooplankton abundance and distribution in 2000. In this paper, we discuss the results of these surveys from 2000 to 2004. Methodology included both multi-frequency acoustic systems and net tows [11]. The survey design included at least three cruises per year from late April to early June.

3 Results

3.1 Herring

The first survey in 1993 documented that the adult herring population had collapsed. The predicted biomass of adult herring was 134,000 t, but we measured only 19,000 t. Subsequent to 1993, the biomass has fluctuated between 7,000 and 37,000 t. After a decade of acoustic surveys, we discovered a strong correlation between the acoustic estimates and an aerial survey index of the accumulated miles of herring spawn (milt) along beaches that had been collected since 1973. We used our acoustic data to convert the index to an absolute estimate of herring biomass, and hindcast the population trend back to 1973 [8]. Subsequent research linked the collapse to the 1989 "Exxon Valdez" oil spill (EVOS) [9]. Both the historical hindcast and the acoustic surveys demonstrated strong impacts of the herring population on seabird and marine mammal abundance [9,12]. We conducted 18 synoptic aerial surveys of foraging Steller sea lions in conjunction with acoustic herring surveys between 2000 and 2006 [8]. The synoptic counts of Steller sea lions were positively correlated ($p \leq 0.01$) with the abundance of the prespawning herring concentrations as estimated from our acoustic surveys (Fig. 1). On a longer time-scale, we found a positive correlation ($p \leq 0.01$) between the agency counts of Steller sea lions in the greater PWS region (including adjacent rockeries) between 1973 and 2004 and our corresponding hindcast of herring abundance (Fig. 2).

There is also a broader geographic scale associated with the collapse of the PWS herring population that followed the oil spill. There are no rookeries within PWS, so the abundance trends of Steller sea lions that we examined primarily represent geographic changes in foraging behavior rather than overall population trends. However, a catastrophic local impact can have long-term impacts on a predator population. We compared all agency census sites for Steller sea lions in the Gulf of Alaska (GOA) that were in common to both 1989 and 2000. There was an overall pattern of decline. When we partitioned the decline by geographic area, we found the magnitude of decline was a direct function of distance from PWS: 86% in PWS, 72% in the remaining eastern GOA, 62% in the central GOA and only 29% in the western GOA (Fig. 3).

There are also strong co-occurrences between winter aggregations of adult herring and other marine mammals and seabirds, including humpback whales, harbor seals, pelagic cormorants, common murres, glaucus-winged gulls, common mergansers, and several loon and grebe species. Not all these relationships have been fully quantified.

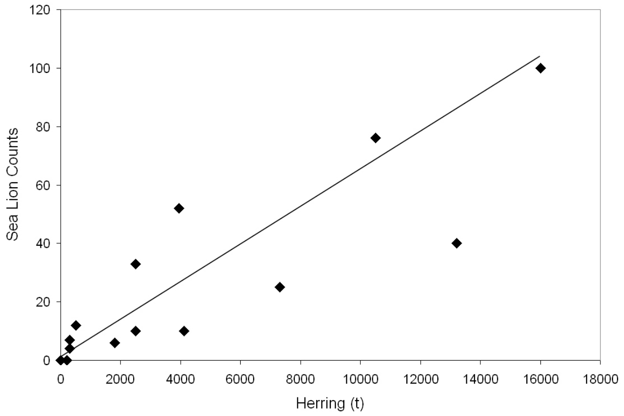

Fig. 1. Comparison of herring biomass estimates from acoustic surveys and synoptic aerial counts of foraging Steller sea lions in various regions of Prince William Sound, 2000-2006.

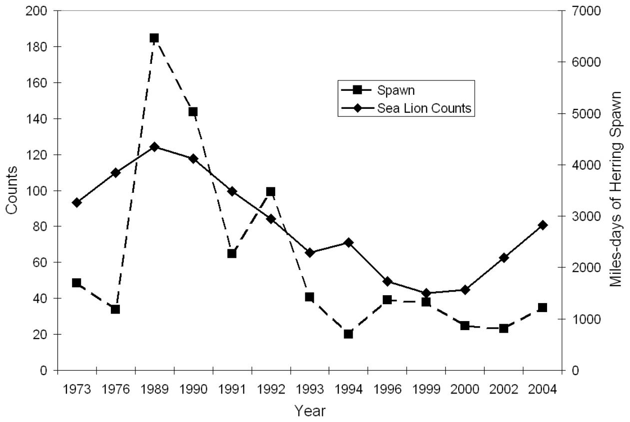

Fig. 2. Comparison of agency counts of Steller sea lions in the greater PWS region from 1973 to 2004 with corresponding herring abundance.

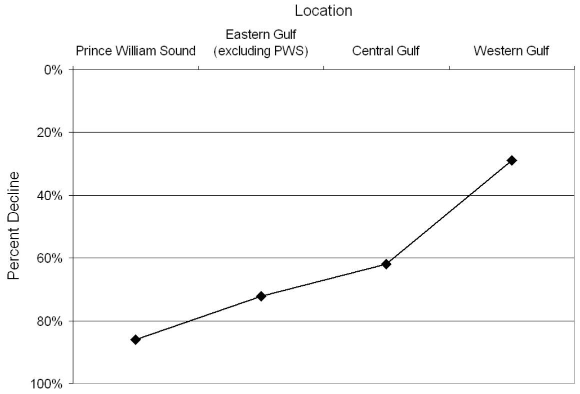

Fig. 3. The magnitude of the decline of Steller sea lions abundance between 1989 and 2000 as a function of relative distance from Prince William Sound.

3.2 Pollock

The first acoustic estimate of the PWS adult pollock in 1995 was 38,000 t. The biomass peaked in 1998, and then began a significant decline through 2003 [11]. Unlike herring, which showed strong associations with seabirds, Steller sea lions and whales, there were no apparent associations between pollock abundance and distribution with any seabirds or marine mammals [11]. However, there is general evidence that trends in the abundance of large benthic fishes, such as arrowtooth flounder and Pacific sleeper and sixgill sharks, are linked to pollock abundance [13],

During spring, some pollock clearly migrate into surface waters to feed on Neocalanus, and move further into nearshore waters to feed on small fishes, including juvenile pink salmon and herring. This inshore movement is greater when Neocalanus is in low abundance (Fig 4). Less documented, but clearly present, is a movement of some pollock into shallow bays and inlets during winter, where they remain near the bottom and prey on juvenile fishes, like herring. This movement may result from low abundance of euphausids, which are the dominant large zooplankton in the deep central basins during winter.

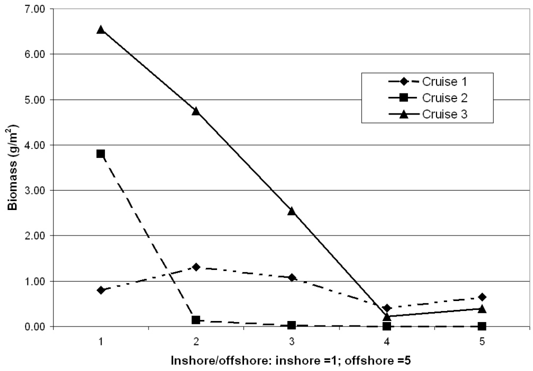

Fig. 4. Progressive shoreward movement of herring and pollock during spring 2001, a year when large copepod abundance was low.

3.3 Large-Bodied Copepods

The Sound Assessment Program (SEA) indicated that pink salmon survival was positively correlated to the abundance of large-bodied copepods and negatively correlated with pollock [5,14]. Pink salmon are a convenient means to judge spring rearing conditions in PWS because they are 2-year fish that outmigrate in the first year, and return and are enumerated in the second year. The SEA Program showed that the dominant adult stocks of herring and pollock used the Neocalanus copepods, euphasids and pteropods in the spring bloom as a primary source of forage. In 1996, we estimated the Neocalanus copepod biomass in PWS to be about 50,000 mt, which may also be an appropriate guess for the biomass of pteropods and euphausids. Our subsequent surveys showed relatively high abundance of large-bodied copepods in 2000, 2002 and 2004, and low abundance in 2001 and 2003. Pink salmon survival generally reflected the abundance of the large copepods, but the correlation was not significant. Further investigation showed a significant increase in pink salmon survival relative to large copepod abundance ($p \leq 0.05$). This significantly increasing survival corresponded to a significant decline in the PWS pollock biomass [11]. Over 80% of the variability around pink salmon, survival between 2000 and 2004 could be accounted for by the relative abundance of large copepods and pollock.

4 Discussion

Bottom-up biological forcing is a mechanism that is borrowed from terrestrial ecosystems where long-lived plants represent 90% of the trophic structure biomass and are the primary source of carbon for higher trophic levels. However, in the marine environment plant biomass represents less than 1% of the trophic structure biomass in the oceans and is very short lived [6]. Plants may determine the amount of new carbon that is introduced to the ecosystem, but they are not the major source of carbon storage, which reduces their role in biological forcing. Even the secondary producers in the marine ecosystem, the grazers, are limited in the amount of carbon storage they can maintain since they are primarily one and two year animals. The first trophic level that is dominated by long-lived (10-20 years) animals that can store multiple years of carbon production in their biomass is the planktivorous fishes. This suggests that the marine trophic structure is far more efficient at incorporating new carbon into higher trophic levels than the terrestrial ecosystem, and that the planktivorous fishes in the middle of the food web are the most likely major forcing agents rather than primary production.

The observations made during and subsequent to SEA program in PWS suggest that two species, herring and pollock, are the dominant wasp waist species and the primary source of biological forcing. Herring was dominant prior to the EVOS [9]. Pollock is now dominant [11]. The returning pink salmon adults are a transient dominant biomass since they rear in the Gulf of Alaska and only spend a month as adults migrating through PWS. Their role is an object of current research.

By shear magnitude, the relative abundance of pollock and herring has major impacts on the structure of the PWS ecosystem. From November through March, adult pollock are distributed primarily in deeper basins adjacent to the Gulf of Alaska and at depths between 175 and 300 m. In contrast, herring are distributed in protected bays and inlets at depths of 10-40 m [8,10]. Many marine mammals and seabirds depend on herring for winter-period forage [10,12]. For example, while Steller sea lion numbers were positively correlated with herring abundance from synoptic aerial and acoustic surveys [11], only one Steller sea lion was ever detected above pollock concentrations in PWS throughout six years of extensive, winter-period aerial and vessel surveys. The lack of co-occurrence between the warm-blooded, air-breathing wildlife predators at the surface and pollock probably results from the winter-period distribution of pollock. Surface conditions are formidably inclement in these deep and offshore areas. In contrast, the herring are distributed near-surface and near-shore within protected bays and fiords of the Sound.

However, pollock is a major predator on other fishes, as well as macrozooplankton in the spring. Our results corroborate previous research that pollock predation is moderated by the abundance of macrozooplankton [14]. For example, a high euphausid abundance tends to keep postspawning pollock in the deep central basins. Typically, pollock move into surface waters in early spring to feed on Neocalanus unless the Neocalanus is in low supply. It is likely that pteropods, which become abundant in late spring/summer, also serve to moderate pollock predation on juvenile fishes. As long as the euphausids, copepods and pteropods are in high enough supply to keep the pollock occupied, the macrozooplankton offer juveniles of species like pink salmon a shelter from predation, and a chance for high recruitment. Our data on predator distributions support the prey sheltering hypothesis, which identifies walleye pollock as a primary predator of juvenile pink salmon, and Pacific herring as a secondary predator.

As in other wasp-waist ecosystems, the two dominant fishes are spilt between one that prefers more near-shore habitats and one that is pelagic. In the PWS case, the pollock is the pelagic species and the herring is more inshore. Due to their diet preferences, they have substantial overlap in time and space to promote competition and predation. Furthermore, these species may alternate in abundance in the Gulf of Alaska similar in manner to sardine and anchovy in the upwelling areas [6]. There was a clear dominance by herring until the mid 1960, when pollock became dominant (Fig. 5). Such changes would have dramatic effects on the abundance of other species in the ecosystem, such as Steller sea lions.

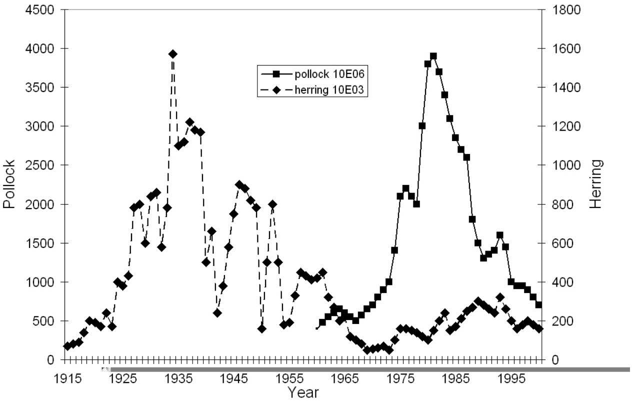

Fig. 5. Comparative abundance of walleye pollock and herring in the Gulf of Alaska, 1915-2000.

These dominant wasp waist fishes and spring macrozooplankton all have annual requirements for carbon that are hundreds of times greater than the juvenile fish cohorts, so they are the obvious large biological signals that need to be measured to determine both the changes in their own biomass and loopholes in the predation matrix that allow some species of juvenile fishes to survive [15]. Given the incredibly high and variable mortality associated with the early life history of marine fishes, it makes much more sense that their numbers are regulated by predation than by the traditional concept of spawning abundance. Now that acoustical-optical methods and practical mechanisms for ecosystem function are emerging, we might see the replacement of the largely unsuccessful historical fisheries spawner-recruit models with new predation recruit models of fish stock dynamics [16].

5 Conclusions

The development of the wasp-waist mechanism for marine trophic systems has helped to clarify the differences between terrestrial and marine ecosystem function. Plants drive terrestrial systems and planktivorous fishes drive marine systems. Before this development, the literature was replete with failed attempts to apply bottom-up mechanisms using primary production to predict the dynamics of top predators and top-down mechanisms using top predators to predict primary production. When you realize how just a couple of species can dominate the wasp waist, it is clear why such predictions fail. The bulk of the production goes only one or two species, and if you do not understand this dynamic the transferred production becomes untraceable. Thus it is likely that long-term population changes in marine ecosystems will only be understood by understanding the roles of the dominant wasp-waist fishes and the associated causal relationships between predators and prey.

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References

[1] V. Cullen, (Ed.) "Global ecosystem dynamics". Joint Oceanographic Institutions, Inc. Washington D.C. 131 pp., (1989).

[2] GLOBEC. "Workshop on acoustical technology and the integration of acoustical and optical sampling methods". Global Ecosystem Dynamics. Report Number 4. Joint Oceanographic Institutions, Inc. Washington D.C. 58 pp., (1991).

[3] GLOBEC. "Initial science plan". Global Ecosystem Dynamics. Report Number 1. Joint Oceanographic Institutions, Inc. Washington D.C. 93 pp., (1991).

[4] G. Thomas, V. Patrick, J. Kirsch and J. Allen. Development of a multi-species model for managing the fisheries resources of Prince William Sound, In D.A. Hancock, D.C. Smith, A. Grant and J.P. Beumer. *Developing and Sustaining World Fisheries Resources - the State of Science and Management*, 2nd World Fisheries Congress. CSIRO Publishing, Collingwood, Australia. pp 606-613, (1997).

[5] T. Cooney, J. Allen, M. Bishop, D. Eslinger, T. Kline, B. Norcross, C. Mcroy, J. Milton, J. Olsen, V. Patrick, A. Paul, D. Salmon, D. Scheel, G. Thomas, S. Vaughan and M. Willette, "Ecosystems controls of juvenile pink salmon (Onchorynchus gorbuscha) and Pacific herring (Clupea pallasi) populations in Prince William Sound, Alaska," *Fish Ocean* 10 (Suppl 1):1-13, (2001).

[6] P. Cury, L. Shannon and Y. Shin. "The functioning of marine ecosystems," In Responsible Fisheries in the Marine Ecosystem, M. Sinclair and G. Valdimarson, Eds. Cambridge, MS: CABI Publishing, (2003).

[7] J. Rice. "Food web theory, marine food webs and what climate change may do to northern marine fish populations," in Climate Change and Northern Fish Populations. R. Beamish Ed. Can. Spec. Publ. Fish. Aquat. Sci. vol. 121, pp 561-568, (1995).

[8] G. Thomas and R. Thorne, "Acoustical-optical assessment of Pacific herring and their predator

assemblage in Prince William Sound, Alaska". *Aquatic Living Resources* 16:247-253, (2003).

[9] R. Thorne and G. Thomas. "Herring and the 'Exxon Valdez' oil spill: an investigation into historical data conflicts". *ICES Journal of Marine Science* 65(1):44-50, (2008).

[10] G. Thomas and R. Thorne, "Night-time Predation by Steller Sea Lions". *Nature* 411:1013, (2001).

[11] R. Thorne. Walleye pollock as predator and prey in the Prince William Sound ecosystem. In: G.H. Kruse, K. Drinkwater, J.N. Ianelli, J.S. Link, D.L. Stram, V. Wespestad and D. Woodby (eds), Resiliency of gadid stocks to fishing and climate change. Alaska Sea Grant, University of Alaska, Fairbanks (16 p.), (2008).

[12] D. Irons, S. Kendall, W. Erickson, L. McDonald and B. Lance. "Nine years after the EXXON VALDEZ oil spill: effects on marine bird populations in Prince William Sound, Alaska," *The Condor* vol. 102, pp. 723-737, (2000).

[13]] Dorn, Martin, Kerim Aydin, Steven Barbeaux, Michael Guttormsen, Benard Megrey, Kally Spalinger, and Mark Wilkins. 2008. 1. Gulf of Alaska Walleye Pollock. NPFMC Gulf of Alaska SAFE. Pages-51-153.

[14 M. Willette, T. Cooney, V. Patrick, D. Mason, G. Thomas and D. Scheel, "Ecological processes influencing mortality of juvenile pink salmon (Onchorynchus gorbuscha) in Prince William Sound, Alaska,". *Fish Ocean* 10 (Suppl 1):14-41, (2001).

[15] Bakun, A. and K. Broad. Environmental 'loopholes' and fish population dynamics: comparative pattern recognition with focus on El Nino effects in the Pacific. Fish Ocean 12:458-473. 2003.

[16] Ricker, W.E. 1962. Regulation of the abundance of pink salmon populations. In Symposium on pink salmon. Edited by N.J. Wilimovsky. The University of British Columbia , Vancouver. B.C. pp 155-210.