Juvenile herring remain in shallow coastal areas for about 3 years before joining adult winter aggregations. Apparently, for the older juveniles, the amounts of plankton in late March and April are also critical determinants of their year-class strength. Winter starvation continues to be a risk, but not as much as it is for the age-0 fish.

For most fishes, losses are greatest in the youngest stages and decrease with age. For Pacific herring in Prince William Sound, it has been estimated that the percentage of survival is lowest for the period of the larval drift (1–7%), but most variable for the period of winter starvation (5–99%) (Norcross and Brown, 2001). All of the early life stages play some role in ultimately determining the recruitment strength of a year-class. In addition to the interaction of the usual limiting factors (the growth environment, predators, and human causes), disease can also play a big role in determining the production status of Pacific herring populations over time. In Prince William Sound, viral hemorrhagic septicima (VHS) and other pathogens have apparently prevented the recovery of stocks damaged by the oil spill of March, 1989 and resulted in reduced or cancelled fisheries in many years following that disaster (Marty et al., 1998).

2.5.5. Walleye Pollock
Kevin M. Bailey and Lorenzo Ciannelli

Introduction

Walleye pollock, *Theragra chalcogramma*, typifies marine fish species that are highly fecund, producing millions of eggs per individual spawner, and which have highly variable mortality rates in early life. A consequence of this strategy is fluctuating annual recruitment (abundance of individual year classes in the fishery; Fig. 2.36) that must be buffered by the averaging effect of many age classes in the population. These life history adaptations allow walleye pollock to take advantage of episodic favorable environmental conditions and thrive by maximizing reproductive success and minimizing mortality. On the other hand, pollock employ a complex array of adaptations to their environment (Olla et al., 1996), only some of which are understood. Pollock has not always been the dominant species in North Pacific ecosystems, but its current success may be the product of a unique match between life history and a combination of environmental conditions. In contrast to the success of pollock in the North Pacific, its congener *Theragra finmarchica* is hardly abundant in the Atlantic Ocean, being a relatively rare catch in the Barents Sea. Two intriguing questions are: How have the opportunities for these congeneric species differed? Why are their abundances contrasting in the two oceans?

Pollock is currently a key species in northern North Pacific ecosystems in the sense that its dynamics influence trophic levels above and below it. For example, declines of pollock have been linked by some scientists to the collapse of the Steller

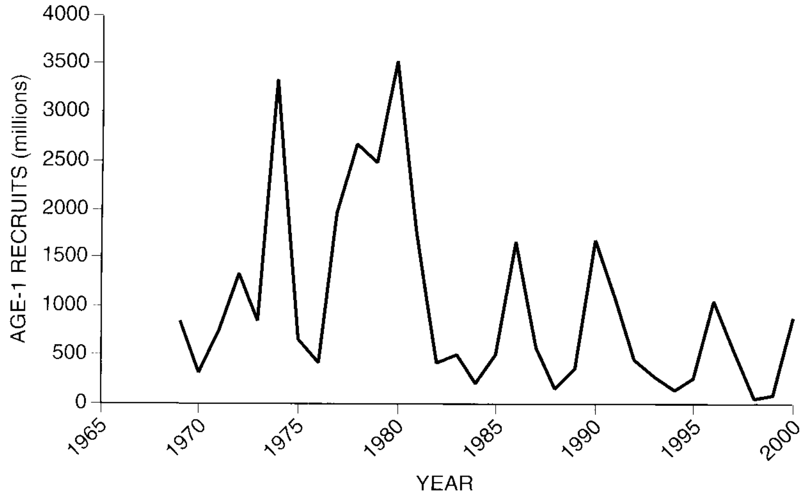

Figure 2.36: Year-class strength of walleye pollock in the western Gulf of Alaska, 1969–2000, determined from virtual population analysis (VPA) (from Bailey et al., 2003).

sea lions in the Gulf of Alaska (Merrick et al., 1997), bird mortalities (Springer, 1992), and to broader and more complex changes in ecosystem structure (Estes et al., 1998). As a major predator, pollock remove a lot of prey organisms, most noticeably competing with humans for valued species such as shrimp and juvenile salmon. In this sense, pollock may be a "waistband" species (Cury et al., 2000), whose dynamics regulate the structure of the ecosystem through both top-down and bottom-up effects (see Box 6.2 for a discussion of the oscillating control hypothesis).

After an ancestral gadoid form invaded the North Pacific Ocean during the Pliocene period some 3 million years ago, pollock gained a strong foothold by adopting a generalist strategy, as opposed to niche specialization. Pollock (Fig. 2.37) thrive in temperatures from about 1 to 10°C in habitats as diverse as eelgrass beds in Puget Sound to the open ocean environment of the Aleutian Basin; it feeds on a variety of prey, from planktonic crustaceans and fishes to benthic clams and worms, and virtually everything taxonomically in between. Pollock inhabit and generally dominate ecosystems from Puget Sound to the northern Bering Sea, and across the Pacific Ocean from the Sea of Okhotsk to the Korean Peninsula.

Of course, pollock populations wax and wane through time, so their own impact on ecosystem structure may be greater or less through time. Their abundance may be influenced by both natural environmental and biological factors and by

Figure 2.37: Juvenile walleye pollock *Theragra chalcogramma* (photograph courtesy of the Japan Agency for Marine-Earth Science and Technology, JAMSTEC).

human harvesting. Unfortunately, we have only observed one complete cycle of the pollock saga, in the Gulf of Alaska from historical lows in the 1960s to a high in the early 1980s, declining to another low in the 1990s through the present. Pollock in Puget Sound have undergone a more dramatic swing in amplitude, dominating groundfish populations in south Puget Sound in the 1980s and then becoming virtually extinct in the 1990s. Because the time series of pollock abundance is so short, our knowledge of how pollock populations respond to the environment and to self-regulation has a low degree of statistical confidence.

Adaptations for Survival

Strategies that the species uses for survival must account for conditions that maximize reproduction and increase survival. The processes that maximize survival and reproduction interact with density-dependent forces within the pollock population to regulate its numbers.

Strategy: maximizing reproduction

Reproductive strategy involves development of reproductive capacity and constraints. Pollock mature at 3–4 years of age, and every individual female produces millions of eggs every spawning season. Pollock are iteroparous (spawning successive annual batches), determinate (a fixed number of eggs spawned per season), and partially synchronous (multiple stages of eggs in the ovaries spawned in clutches). An individual female may spawn her eggs in several clutches over a period of days and up to 14 clutches over the period of a month. Eggs are released into the water and fertilized by paired males after an elaborate courtship. Eggs are spherical, about 1.0 mm in diameter, take about 2 weeks to hatch at 6°C, and have enough yolk for hatched larvae to survive for about a week without feeding.

Another strategic aspect of reproduction is selection of a spawning site. The spawning locations and the geographic range of the pollock distribution are probably bounded by the environmental conditions that allow the survival of pollock eggs and larvae. Some species have adapted to conditions at the spawning location to minimize the number of eggs and larvae being swept away by ocean currents by developing strong swimming capabilities (Leis and Carson-Ewart, 1997). However, pollock larvae are very weak swimmers for the first few weeks and are unable to effectively swim against the strong Alaskan currents. In order to make up for their weak swimming ability, coastal stocks of pollock broadcast their eggs in deep inshore bays or in sea valleys and canyons that penetrate the continental shelf, which tend to have oceanographic features that favor retention of eggs and larvae over the shelf and near favorable nursery sites (Bailey et al., 1999). In more oceanic stocks, such as in the eastern Bering Sea, they tend to spawn where currents are very weak, or where transport into favorable nursery areas is climatologically (on the average) probable. The spawning regions of pollock are noted for mixing of coastal and nutrient-laden oceanic waters and stratification of the water column, leading to enhanced productivity; these conditions favor the survival of early life stages of pollock. In the Gulf of Alaska, pollock typically spawn during the last week in March and first week in April in the Shelikof Strait (Fig. 2.38). In this area, mixing of the Alaska Coastal Current, the Alaskan Stream, and coastal water, along with springtime increases in sunlight and water column stratification, leads to an intense spring bloom and reproduction of zooplankton. Zooplankton prey of pollock larvae are further concentrated by physical features, such as eddies and fronts (Napp et al., 1996), leading to favorable feeding conditions. Finally, late larvae and juvenile pollock are carried toward favorable nursery areas, such as the waters around the Shumagin Islands.

How adult pollock find their way back to these established spawning areas is currently unknown and controversial (Bailey et al., 1996). Whether there is natal philopatry (return to birth location) or spawning philopatry (return to a previous spawning site used by adults), either through genetic adaptation, imprinting, or social facilitation (learning), should play a role in how stocks are managed. Natal philopatry is a strategy to maximize the probability that the offspring will find suitable and persistent nursery habitats. In contrast, spawning philopatry through social facilitation would allow the population to capitalize on more ephemeral environmental conditions. Thus, the prevalence of one (natal philopatry) over the other (spawning philopatry) homing mechanism may depend on the variability of the surrounding environment.

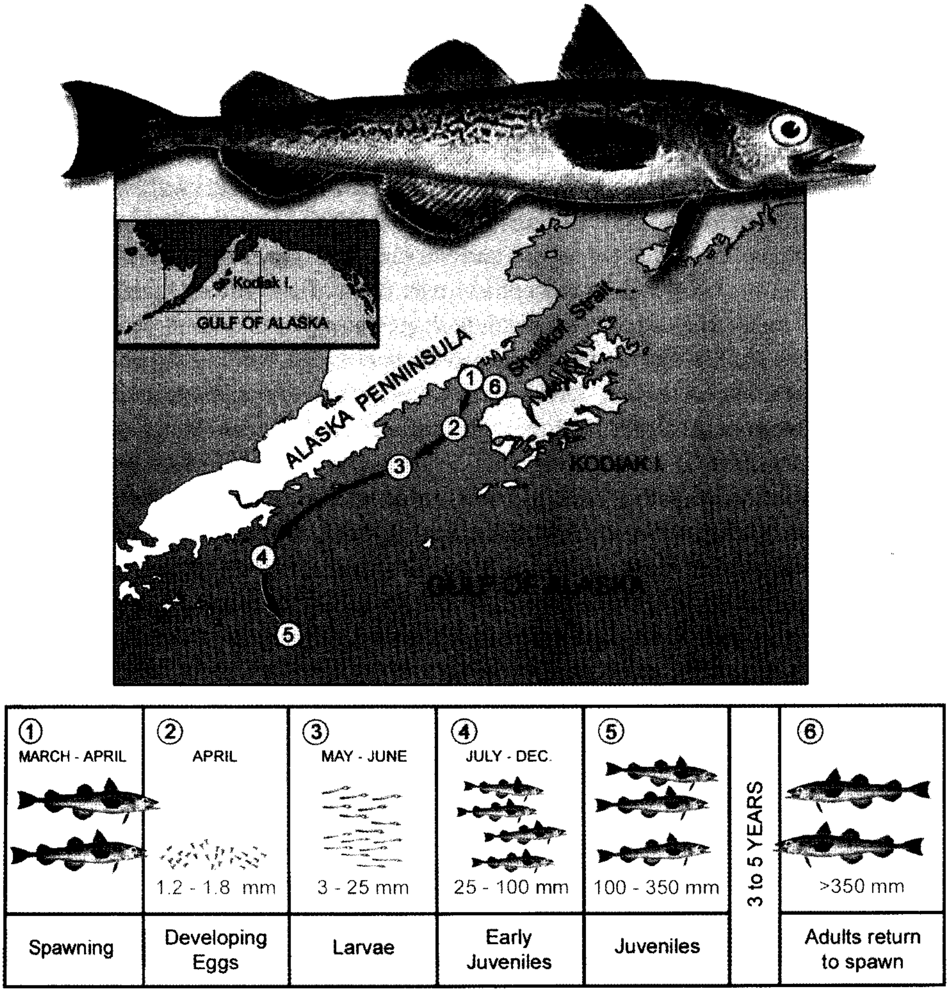

Figure 2.38: Life cycle of walleye pollock in the western Gulf of Alaska showing spawning (1) and juvenile rearing areas (2–5) in top panel. The sizes and timing of various stages are shown in the bottom panel.

We know that the bulk of pollock spawning in the Gulf of Alaska has historically been highly concentrated in the Shelikof Strait. However, in recent years, pollock spawning appears to have shifted in location, and the Shelikof Strait aggregation is no longer dominant. New and large pollock aggregations have been recently found near the Shumagin Islands and the Unimak Bight.

Strategy: minimizing mortality

Mortality rates of pollock eggs and young larvae are very high, ranging from 4 to 40% per day, but decline as the pollock develop (Fig. 2.39). In fact, larval condition can vary from year to year and by location, and a high percentage of larvae in the ocean has been observed to be in poor feeding condition (Theilacker et al., 1996). Studies have shown that egg and early larval development and survival is suboptimal at temperatures below about 0°C and above 10–12°C. Extremely high and low temperatures can be lethal to eggs and larvae, but generally for the Gulf of Alaska population, which is in the central part of its distribution, higher temperatures (6–7°C) tend to favor better survival, perhaps through one or more indirect mechanisms (Bailey, 2000). Optimal prey levels for successful feeding depend on many different conditions, including larval size, temperature, light levels, turbidity, and turbulence (Porter et al., 2005), but they generally range between 20 and 40 prey/liter (Theilacker et al., 1996).

Growth variation is another strategy to minimize mortality. Faster growth rates may lead to lower mortality under some conditions (Anderson, 1988). According to Houde's (1987) stage duration hypothesis, faster growth through early stages that are vulnerable to mortality is beneficial. This concept has been difficult to show in pollock larvae. There is some evidence that strong year-classes of pollock have attained a greater size-at-age as early juveniles (Bailey et al., 1996). Pollock eggs and larvae are also lost by predation to many different types of invertebrate planktonic predators; unfortunately, these organisms masticate their prey, making the quantification of the

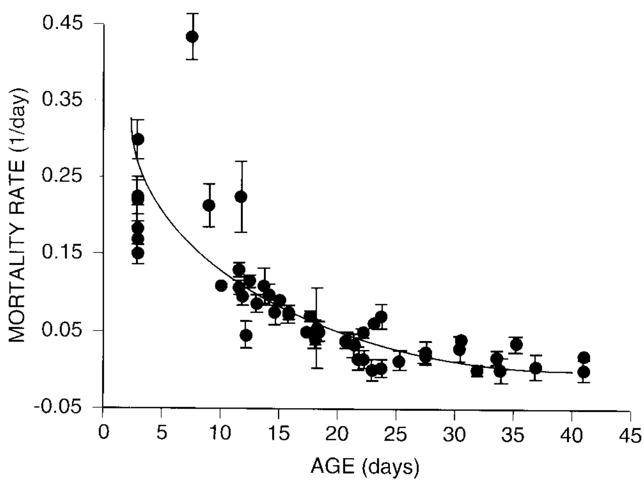

Figure 2.39: Mean mortality rates of walleye pollock eggs and larvae determined in field studies as the difference in abundance of daily cohorts between survey periods (from Bailey, 2000).

predation rate difficult. Immunological detection of pollock as prey, using anti-pollock antibodies, has been employed to identify pollock eggs and early larvae in the guts of amphipods, euphausiids, and mysids. Visual inspection of predator guts has been used to detect pollock eggs and larvae in the guts of eulachon, capelin, and adult pollock. Adaptive strategies of pollock to reduce predation loss are numerous, including: transparency of eggs and early larvae, low swimming speeds that minimize encounters with predators, lack of motion making them less easily detected by visual and mechanoreceptive predators, and deep-water habitat where there is little light and few predators.

At later stages, predation on juveniles is an important source of loss to the population. Piscivorous fishes, including halibut, cod, arrowtooth flounder, and flathead sole, contribute to significant mortality (Livingston, 1993). Juvenile pollock are also prey to marine mammals and birds. As described in the following section, changes in ecosystem structure and the abundances of these predators can have important consequences to pollock population dynamics. The high variability of pollock abundance may be an adaptive strategy to run the gauntlet of predators awaiting them, thereby overwhelming the predation capacity of the community when larvae are abundant.

Ultimately, with a successful and dominating population such as pollock, density-dependent processes may either enhance or inhibit population increases. At high levels of abundance, pollock may outrun their prey supplies (Anderson et al., 2002), leading to slower growth, delayed maturity, and decreased reproductive success. At high densities of pollock, predators may also undergo changes (swarming, shift feeding behavior, increase recruitment, etc.) that lead to density-dependent mortality. Cannibalism is also an important regulative process in pollock, especially in the Bering Sea (Dwyer et al., 1987). In the Gulf of Alaska system, cannibalism is not as prevalent, and it may be minimized by the relatively nonoverlapping distributions of adults and juveniles (Shima et al., 2002). In the Bering Sea, the tolerance of juveniles to water <2°C may be an adaptation to provide them with a refuge from adult predators. Thus, there is a complicated scenario of predation and cannibalism in a complex landscape, such as in the Bering Sea, where the population may be self-regulating through cannibalism, but where there is an interaction with thermal refuges, prey availability (Sogard and Olla, 1996), and removal of large predators by fishing.

Effect of Ecosystem Structure on Pollock Survival

Changes in environmental regimes and ecosystem structure may have important effects on factors regulating the recruitment of pollock. For example, in the late 1980s, as the Gulf of Alaska ecosystem apparently shifted from one dominated by pelagic forage fishes and shrimps to a community dominated by piscivorous flatfishes and gadids, a shift occurred in the life history stage at which recruitment of pollock is regulated (Bailey, 2000). Prior to the shift in ecosystem structure, recruitment was correlated with early larval survival, but after the shift, juvenile mortality rates increased and recruitment was regulated by predation mortality of juveniles. Therefore, control points may change from year to year, and depend on longer-term changes in the environment and community structure, such as those occurring with environmental and biological regime shifts.

Environmental and ecosystem structure shifts may also have indirect effects on pollock survival, such as causing changes in the operation of density-dependent mechanisms. For example, Ciannelli et al. (2004) found that the level of density-dependent mortality in juvenile pollock increases when water temperature and predation intensity are high. Statistical models have been successfully employed to describe how the density-dependence structure of the population interacts with high- and low-frequency factors to regulate recruitment. Changes in ecosystem structure may also influence the distribution of pollock, their predators, and prey with consequent effects on pollock production processes. For example, there has been an increase in the abundance of pollock in nearshore small-mesh trawl surveys since the regime shift in the late 1970s (Anderson and Piatt, 1999). At the same time, pollock stock abundance in the Gulf of Alaska has declined precipitously. One might infer from these seemingly conflicting observations that the distribution of juvenile pollock, the stage largely caught by the small mesh trawls, has shifted inshore, making them more vulnerable to the coastal assemblage of predators.

Conclusions

Pollock is an opportunistic species that is able to expand and adapt quickly to different environments. On the other hand, the population is limited by finding and adapting to local conditions that favor successful spawning (maximizing reproduction) and survival (minimizing mortality) of the early life stages. Local populations of pollock respond differently to shifting environmental regimes, as warming periods have seen those stocks at the southern margins of the pollock distribution falter or fail. In the center of its distribution of mass in the eastern Bering Sea, pollock have been (if anything) favorably impacted by periods of environmental warming. In the Gulf of Alaska, the situation appears more complex, as pollock have been initially favored by a warm environmental regime (e.g., stock increase in the late 1970s and mid-1980s), but negatively impacted afterwards in connection with a sharp increase of predator biomass. Pollock spawn once per year, in an event that is highly concentrated in space and time. Given the fragility of eggs and larvae to environmental conditions, and their concentration in space and time, the survival of a whole year-class is vulnerable to the vagaries of the ocean and weather, such as storms passing through Shelikof Strait. On the other hand, pollock dynamics are buffered partly by multiple spawning stocks, spawning in different locales, and by multiple age classes in the population. Spawning in different locations moderates the effects of temporal variation in habitat suitability by taking advantage of spatial variation. The long life span of pollock is an adaptation that tempers the high variation in year-class strength. A high abundance of predators on adults, as well as commercial fishing, which removes older age classes, reduces the age span over which the mean abundance is averaged (and perhaps other aspects of the contribution of older fish to the population's viability). Consequently, the population will be more dependent on fewer age classes, hence contributing to overall stock variability (Longhurst, 2002).

Acknowledgements

Section 2.5.5 is contribution FOCI-0491 to NOAA's Fisheries-Oceanography Coordinated Investigations.

2.5.6. Comparing Fish Life Histories

Theodore Cooney

As we have seen reproductive strategies, food web dependencies, range, and tolerances to the physical environment are addressed by these three fishes in different ways. The remarkable 2-year life span of the pink salmon exploits freshwater and marine habitats, while the herring and pollock are more long-lived, living and reproducing entirely as marine fishes. The pink salmon invests energy in rapid growth and a relatively small number of very large eggs that produce large, sessile larval fish (the alevin), rearing in the protection of the substrates of coastal streams. The alevin is generally a nonfeeding stage, subsisting during the cool coastal winters primarily on yolk-sac reserves for many months. In this way, late summer and fall spawning by pink salmon has apparently evolved to produce a large (30 mm), free-swimming, juvenile stage that enters shallow marine waters during the spring plankton bloom (mid-April) at a time when water temperatures are warming and zooplankton stocks are increasing (Cooney et al., 2001).

In contrast, both the pollock and herring produce large numbers of small eggs – pelagic in the case of pollock and demersal for herring. Pollock spawn in the late winter and early spring in selected shelf and deep-water coastal areas (>200 m), while the herring deposit their numerous sticky eggs on underwater vegetation and other intertidal and shallow subtidal substrates at locations along the coast in early to mid-spring. Larval pollock and herring are tiny (<10 mm), weak swimmers; their distributions are determined primarily by vertical and horizontal currents. Part of the reproductive strategy for pollock and herring is to produce huge numbers of early life stages (eggs and larvae), betting that a few will find the conditions necessary for survival to the juvenile and later stages. It is generally believed that pollock and herring spawn at definite times and in specific locations to place their drifting egg and/or larval forms in currents that usually distribute the developing stages to favorable rearing areas.

LONG-TERM ECOLOGICAL CHANGE IN THE NORTHERN GULF OF ALASKA

Edited by
Robert B. Spies

Elsevier
Radarweg 29, PO Box 211, 1000 AE Amsterdam, The Netherlands
The Boulevard, Langford Lane, Kidlington, Oxford OX5 1GB, UK

First edition 2007

Library of Congress Cataloging-in-Publication Data
A catalog record for this book is available from the Library of Congress

British Library Cataloguing in Publication Data
A catalogue record for this book is available from the British Library

ISBN-13: 978-0-444-52960-2
ISBN-10: 0-444-52960-8

Printed and bound in Italy

07 08 09 10 11 10 9 8 7 6 5 4 3 2 1