Chapter I

FISH STOCK ASSESSMENT AND FISHERIES MANAGEMENT: AN OVERVIEW

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Introduction

A fish population is a group of interbreeding fish that is characterized by its own birth rate, growth rate, age structure, and death rate. A fish stock is often referred to as that portion or subset of a fish population that is subject to exploitation or harvest. Fish stocks may respond differently to exploitation because of differences in reproductive, growth, and natural mortality rates. Therefore, fish stocks are considered discrete units for management purposes.

The purpose of fish stock assessment is to evaluate the status of a fish stock and to predict how the stock will respond to various exploitation or harvest scenarios. The current status of a stock is characterized by estimating stock parameters such as mortality (natural and fishing), abundance, biomass, age structure, and growth rate. The future status of a stock is predicted by modeling the process of stock change over time in response to management, using the previously estimated stock parameters.

Fisheries management is the process by which we attempt to control fish stock abundance by regulating harvest. Fisheries management decisions are made in an attempt to meet predetermined objectives concerning future stock status based on biological, sociological, economic, and political inputs.

The history of fish stock assessment and fishery resource management began with the erroneous assumption that the ocean's resources were unlimited. Thomas Huxley concluded in 1884 that fish were so abundant and fecund, and man's ability to harvest them was so limited, that fish populations were immune to man's activities. Shortly thereafter, at the turn of the century, the International Council for the Exploration of the Sea (ICES) initiated the collection of commercial catch data to respond to concerns of overfishing and depleted fish stocks. World Wars I and II allowed worldwide fish stocks to rebuild, but overfishing in the last fifty years has driven stocks to record low levels.

The most recent Report on the Status of Fisheries of the United States published every year by the National Marine Fisheries Service (NMFS) indicates that 98 fish stocks nationwide are considered overfished. Fisheries managers have the responsibility to properly manage these fish stocks for the long-term benefit of both the fish stocks and the human population. Management decisions are made based on information derived through the various methods of fish stock assessment. Used properly, these methods will allow overfished stocks to rebuild and will ensure harvest pressure does not exceed sustainable levels.

A stock assessment report typically includes the following sections and this introductory chapter provides an overview of each section:

- 1. Description of the fisheries that interact with the stock and the presentation of fishery dependent data (landings, effort, etc.).
- 2. Results of research surveys that provide fishery independent data on abundance and samples for biological analysis.
- 3. Life history characteristics of the resource including natural mortality, growth, and maturity.
- 4. Estimation of population and fishery parameters such as stock-recruitment relationships, exploitation rates, yield, and spawning stock biomass suing assessment models.
- 5. Biological reference points based on the previous models and analyses, and an evaluation of the current status of the stock based on the reference points.
- 6. Review of management objectives and alternative actions to achieve a sustainable fishery, and an evaluation of these alternatives using the models previously developed in a projection mode.

Fishing Gears, Fisheries and Fishery-Dependent Data

A wide array of gear types are used to harvest fishery resources commercially and recreationally. The principal gears are: hook and line, pots and traps, trawls and dredges, seines, and gillnets.

Hooks and Line Gear

Hook and line fishing methods have evolved from the simple act of attaching bait to a line, lowering that line into the sea, then carefully retrieving bait with a prey still attached feeding. This method of fishing is referred to as bobbing and is practiced today in Chesapeake Bay by recreational fishermen using a chicken neck attached to a line for the purpose of harvesting blue crabs.

The modern bent hook is believed to have evolved from a natural thorn hook, and from stone and carved shell hooks. The simplest form of hook and line fishing is the handline. It consists of a line, sinker, leader, and at least one hook. There are both recreational and commercial handline fisheries in the U.S.A. In the New England area, handlines are used to harvest bluefin tuna from small vessels. In fact, although this is a technologically sophisticated fishery with fish finding and navigation electronics, it is still conducted by individual or pairs of fishermen in small boats (< 10 m), so it may be considered an artisinal fishery. Recreationally, handlines are used in ice fishing.

The most basic pole and line fishery is a bamboo pole with a short line and hook attached. Recreationally, these are used to catch small fish in a wide variety of fisheries. The addition of a reel to store the line was a significant improvement to pole and line gear, and is again used in recreational and commercial fisheries. The reel, pole, and line gear is probably the most widely

used recreational fishing gear used in freshwater and marine fisheries in a wide variety of forms from fly fishing to offshore trolling for large pelagic billfish.

With the guiding philosophy that if one hook is good, many hooks are better, commercial fishermen developed bottom longline gear (Figure 1). The principle element of this gear is the mainline or groundline that can extend up to 50 km in length. Branching off the mainline at regular intervals are leaders or snoods, and hooks. Anchors hold each end of the mainline in place and surface buoys attached via float lines to the anchors mark the location of the gear. The mainline was initially constructed of natural fiber lines, that was replaced by a hard-lay, twisted, tarred nylon, and now monofilament and wire cables are typically used. Leaders were initially tied to the mainline, and now they typically snap-on to the mainline allowing separate storage of the hooks and leaders and the mainline. All bottom-set, longline gear, is considered fixed and passive because once deployed the gear does not move and the fish voluntarily takes the hook.

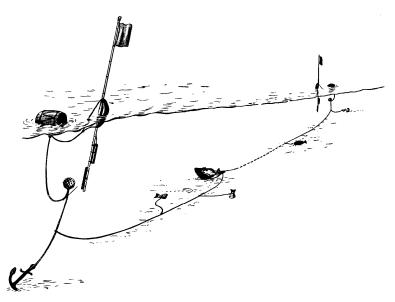


Figure 1. Bottom longline gear (USDOI Circular 48).

An evolution from bottom longline gear was the development of pelagic longline fishing methods. The mainline is suspended at depth from buoys and dropper lines, with the minimum depth (about 20 m), so as to avoid entanglement by coastal maritime traffic. The length of the mainline varies from 30 to 100 km depending on the size of the vessel. The mainline material began as 3-strand twisted, hard-lay, tarred nylon, but has been entirely replaced by monofilament. The line is stored on a reel equipped with a level-winder to prevent tangles on the reels. Hooks, leaders, and dropper lines are stored on small reels end to end.

On the East Coast of the U.S.A., there is an active pelagic longline fishery for large highly migratory pelagic species, in particular, swordfish, tuna, and shark. A typical vessel, 20 m in length, fishes a 100 km mainline and about 500 hooks on a 12 hour soak. The gear is fixed with respect to the water, but can drift over the seabed as much as 100 km in an overnight-soak. The gear is passive, in that fish are attracted to the hook with bait, light sticks, and sometimes noise makers, and voluntarily take the gear.

The art of attracting fish or squid to a lure with hooks moving up and down is called jigging. Jigging is conducted by hand, with a reel, pole and line, or using jigging machines that are programmed to move the lure in a particular way. Finfish usually take the hook with their mouth, but are occasionally snagged. In contrast, squid are almost always snagged by the hooks. Thus, jigs are classified as either active or passive depending on the methods of capture.

Pots and Traps

The essential element of any pot or trap fishing gear is a non-return device that allows the animal to voluntarily enter the gear, but makes escape difficult, if not impossible. The terminology used to identify pots and traps is also confusing, as both terms have been applied to the small portable, 3-dimensional gear. In this manual, a pot is defined as a small, portable, 3-dimensional device, whereas a trap is identified as a large, permanent, 2-dimensional gear.

The principle of operation of pot gear is that animals enter the device seeking food, shelter, or both. The non-return device, while allowing the animal to enter the gear, restricts escape. The holding area retains the catch until the gear is retrieved. Bait is placed in a bag or cage within the pot. Culling rings or escape vents are added to the exterior wall of the pot to allow for the release of undersize sub-legal animals. Finfish, shellfish, and crustaceans are all harvested with pots in the estuarine, coastal, and offshore waters of the U.S.A.

The blue crab fisheries conducted in the inshore waters of the mid and south Atlantic regions use a wire mesh pot (Figure 2). The design of the pot incorporates two sections, an "upstairs" and "downstairs." Crabs attracted by bait enter the "downstairs" via one of two to four entrance funnels. Once in the pot, the escape reaction is to swim upward, so a partition with two funnels separates the two sections. The "upstairs" section serves to hold the catch for harvest. Escape vents or cull rings may be installed in the pot to reduce juvenile bycatch. Crab pots are usually fished as singles and are hauled by hand from small boats or with a pot hauler in larger vessels. Crab pots are generally fished after an overnight soak, except early and late in the season.

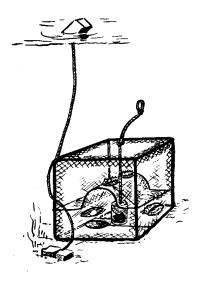


Figure 2. Crab pot (USDOI Circular 48).

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Traps are generally a large scale, 2-dimensional device that uses the seabed and sea surface as boundaries for the vertical dimension. The gear is fixed, that is it is installed at a location for a season, and is passive, as the animals voluntarily enter the gear. Traps consist of a leader or fence that interrupts the coast parallel migratory pattern of the target prey, a heart or parlor that leads fish via a funnel into the bay section, and a bay or trap section that serves to hold the catch for harvest by the fishermen. The non-return device is the funnel linking the heart and bay sections. The bay, if constructed of webbing, is harvested by concentrating the catch in one corner, a process referred to as "bagging" or "hardening" the net. The catch is removed by "brailing" with a dip net. The advantages of traps are that the catch is alive when harvested, resulting in high quality; that the gear is very fuel efficient; and that there is the potential for very large catches. The disadvantages are that the initial cost of the gear is high, that there is competition for space by other users of the estuarine and coastal ecosystem, and finally that the fish must pass by the gear to be captured, so any alterations in migratory routes will radically affect catch.

On the mid-Atlantic coastal plain, large traps constructed of webbing hang from stakes that are pounded into the unconsolidated seabed and are locally referred to as "pound nets" (Figure 3). These traps are usually set at points or capes that fish tend to migrate around. The leader sections are 100 to 600 m in length, starting in shallow water (< 2 m), and ending in water depths of 10 to 15 m. The heart sections lead to single or double funnels that lead into the bay section. The gear captures both pelagic and demersal species.

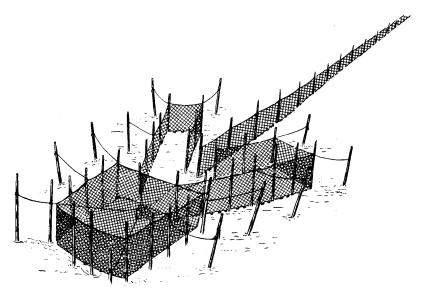


Figure 3. Pound net (USDOI Circular 48).

Dragged Gear

Fishing gear that is dragged or towed over the seabed or through the water is referred to as mobile gear. The dragged gears include a bag constructed of webbing or rings and chain links that collect the catch. These are exclusively active fishing gears, in that the animals do not voluntarily enter the gear, but are either swept up from the seabed or filtered from the water by the gear. Towed gear evolved from the need of man to harvest more efficiently and that required

collecting from more water or the bottom. Towed gear was initially deployed from hand-powered boats, then sailing vessels, and finally from large ships with engines greater than 1000 horsepower. Mechanization of these fisheries with engines and winches enabled larger gear to be towed faster and handled with less labor. The earliest dragged gear was probably some form of small rake used to collect shellfish towed by a hand-paddled canoe. As we enter the twenty-first century, the largest gear is a pelagic fish trawl with a mouth opening in excess of 100 x 100 m, towed by a vessel larger that 100 m with an engine of 2000 horsepower or more.

Dredges are rake-like devices, equipped with bags to collect the catch. They are typically used to harvest molluscan shellfish from the seabed, but occasionally are used to target crustacean, finfish, and echinoderm species. Dredges are designed to harvest both epifauna and infauna; however, the specific design details of the gear are very different.

In estuarine water, dredges are used to harvest oysters. The oyster is a sessile organism, generally growing in reef-like habitats. The oyster dredge consists of a steel frame 0.5 to 2.0 m in width, with an eye and "nose" or "tongue," and a blade with teeth (Figure 4). Attached to the frame is the tow chain or wire, and a bag to collect the catch. The bag is constructed of rings and chain-links on the bottom to reduce the abrasive effects of the seabed, and twine or webbing on top. The dredge is towed slowly (< 1 m/sec) in circles, from vessels 7 to 30 m in length. Compared to shaft tongs or patent tongs, the oyster dredge is very efficient. In many regions, oyster dredging is allowed only on private or leased oyster beds, and prohibited on public beds. However, in the Maryland portion of Chesapeake Bay, dredging is permitted on public beds, but only under sail, so as to maintain inefficiency, thus allowing for a traditional fishery.



Figure 4. Oyster dredge (USDOI Circular 48).

Blue crabs are harvested during the winter months with large dredges similar to oyster dredges. The blue crab, susceptible to pots during the active summer months, are dormant in the winter months, and burrow into soft estuarine bottoms. Stern-rig dredge boats (≈ 15 m in length) tow two dredges in tandem from a single chain warp. The dredges are equipped with long teeth (10 cm) that rake the crabs out of the bottom. This same gear is used to harvest whelk in the summer and mussels in the fall from Chesapeake Bay.

Again, as fishermen sought to increase efficiency and tow vessels became larger, dredges evolved into beam trawls so as to capture finfish. The steel frame became larger and lighter, and the bag became larger and funnel shaped, so as to concentrate the catch in a cylindrical-shaped, webbing section, referred to as the codend. The first beam trawls were towed by sailing vessels, but today large beam trawls with mouth openings of 15 to 20 m, are towed from both sides of modern, high horsepower trawlers.

Otter trawls developed as fishermen sought to further increase the horizontal opening of the trawl mouth, but without the cumbersome rigid beam (Figure 5). In the late 1880s, Musgrave invented the otter board, a water-plane device that when used in pairs, each towed from a separate wire, served to open the net mouth horizontally and hold the net on the bottom. Initially, all otter boards were connected to the wing ends of the trawl, as they are today in the shrimp trawl fishery. In the 1930s, the Dan Leno gear developed by Frenchmen, Vigarnon and Dahl, allowed the otter boards (doors) to be separated from the trawl wing ends using cables or "ground gear." This technology increased the effective area swept by trawls from the distance between the net wings to the distance between the doors. The ground gear can be as long as 200 m, thus increasing the area swept by the trawl by as much as three fold.

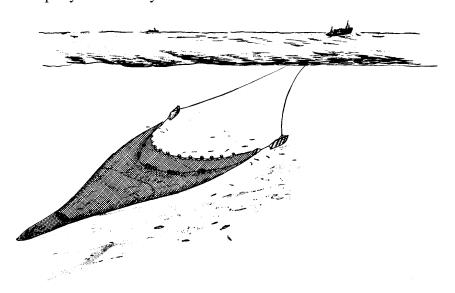


Figure 5. Otter trawl (USDOI Circular 48).

Bottom trawl fisheries are prosecuted for demersal species on all coasts of the U.S.A. In the northeast, vessels from 15 to 50 m fish in waters ranging from 10 to 400 m in depth. Small mesh nets are used to capture northern shrimp, whiting, butterfish, and squid. Large mesh trawls are used to harvest cod, haddock, flounder, and other large species. These trawls are typically rigged with long ground wires that create sand clouds on the seabed, herding the fish into the trawl mouth. In the southeast and Gulf coast areas, small mesh trawls are used to harvest shrimp.

Pelagic fishes are harvested using off-bottom or midwater trawl nets. The nets must be aimed or directed at specific concentrations of fish. Therefore, the fishermen must be able to identify the location of fish both laterally and vertically, and to direct the pelagic trawl to that position.

Seines

Fishing gear that is used to encircle marine resources either on the seabed or in the water column are classified as surround gear. Because the area enclosed by the gear is limited, the gear is directed or aimed at identified concentrations of fish. Surround gear are often referred to as seine nets.

The simplest form of seine is a single wall of webbing without a bag, connected at each end to poles that are handled by fishermen. The net is pulled through the shallow water collecting finfish, crustaceans, mollusks, etc., and finally dragged up onto a beach where the catch is sorted. The webbing is of variable mesh size, but is usually very small, (about 0.5 cm), as the gear is typically used to harvest bait fish for recreational hook and line fisheries. Typically a recreational or subsistence beach seine is about 20 m in length and 1.0 to 1.5 m in height with a 1.0 cm mesh size. Commercial beach seines range in length from 200 to 400 m and are equipped with a bag in the center or side.

The long-haul seine is set and hauled in shallow water estuaries from a boat (about 15 m). The net is a single wall of small mesh webbing (< 5 cm) and is usually greater than 400 m in length and about 3 m in depth. The end of the net is attached to a pole driven into the bottom and the net is set in a circle so as to surround fish feeding on the tidal flat. After closing the circle, the net is hauled into the boat, reducing the size of the circle, and concentrating the fish. Finally, the live fish are brailed or dip-netted out of the net.

Seine nets are also used on pelagic fishes. However, the net must be designed to close at the bottom. The nets are floating, that is the buoyancy on the float line exceeds the weight of the webbing and leadline. The gear fishes from the air-sea interface to the depth of the webbing. The gear is set in a circle around an identified school of pelagic fishes then closed off on the bottom, so as to prevent the escape of the fish.

The purse seine is closed using a continuous purse line (Figure 6). Functionally, purse seines are used to surround a concentration of fish, then the purse seine is hauled in so as to close the bottom of the net.

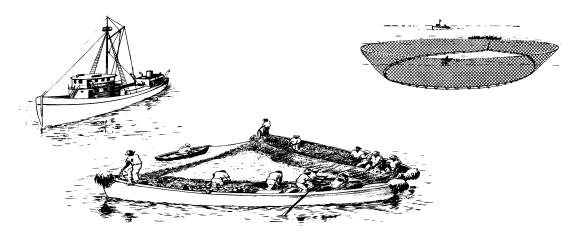


Figure 6. Purse seine (USDOI Circular 48).

The puretic power block developed in the early 1950s, was a significant mechanization of the purse seine fishery. The V-shaped sheave, attached to a beam end and powered by a hydraulic motor, has replaced 10 to 20 men that used to haul in the long wings of the small seines (300 m) used to harvest menhaden in Chesapeake Bay. The largest purse seines now used on tuna, fish in the open ocean and are more than 2000 m in length and 200 m in depth. Without the power block, these fisheries would not have developed.

Gillnets

Gillnets include a group of fishing gear types where animals are captured by a wall of webbing in the water column or on the bottom. The animals are captured by wedging, gilling, or tangling.

Gillnets operate principally by wedging and gilling fish, and secondarily by entangling. The nets are a single wall of webbing with float and lead lines. The nets are designed and rigged to operate as either sink or floating nets, and are anchored or drifting. The webbing is usually monofilament nylon due to its transparency; but multifilament, synthetic or natural fibers, are also used.

Anchored sink gillnets are used to harvest demersal fish along all coasts of the U.S. The nets are rigged so that the weight of the leadline exceeds the buoyancy of the floatline, thus the net tends the seabed and fishes into the near bottom water column (Figure 7). Anchors are used at either ends of the net to hold the gear in a fixed location. The nets vary in length from 100 to 200 m and in depth from 2 to 10 m. Multiple nets are attached together to form a string of nets, up to 2000 m in length. In shallow water, sink gillnets may fish from bottom to surface, if the webbing is of sufficient depth.

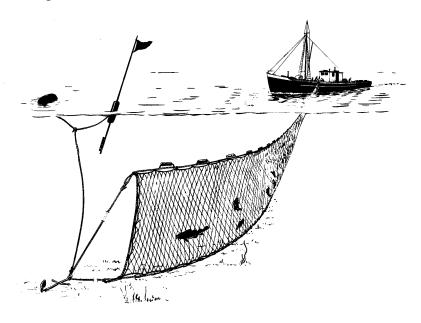


Figure 7. Sink gillnet (USDOI Circular 48).

Gillnets are also designed so as to float from the sea surface and extend downward into the water column and are used to catch pelagic fish. In this case, the buoyancy of the floatline exceeds the weight of the leadline. Floating gillnets are anchored at one end or set-out to drift usually with the fishing vessel attached at one end. Anchored floating gillnets are used in shad fisheries on the East coast. Offshore, large mesh drift nets are set for swordfish and other large pelagic fishes.

Fishery-Dependent Data and Analyses

The National Marine Fisheries Service (NMFS) and state agencies collect catch and effort data on the recreational and commercial fisheries, so as to monitor the status of the fishery resource stocks and to estimate fishing mortality. From these data and analyses, and in conjunction with fishery independent data sources (scientific surveys) and analyses, fishery scientists are able to predict the outcomes of various management alternatives.

In the commercial fisheries, landings data is collected from fishermen's logbooks and trip tickets, dockside interviews by port agents, monthly summaries from dealers, etc. However, landings data may not reflect catch due to at-sea discards. Data on discards is collected by at-sea observers who sample the entire catch, then note discards and landings. Sea- sampling is usually only conducted on a subset of the fishing fleet due to the high cost of staffing these programs, but the observed discard rates are extrapolated to the entire fleet, so as to develop complete estimates of age/size-specific catch. Discards are prorated into the landings based on their age/size and gear-specific survival probability. Effort in commercial fisheries is based on license data according to gear type, vessel tonnage, days at sea or fishing, the amount of gear set and soak time, etc. Within a specific fishery, there is a standardized unit of effort, for example, one day fishing by bottom trawl for a 50 to 99 ton vessel. Other classes of trawl vessels, both smaller and larger, are then compared to the standard vessel in terms of catchability and rated accordingly.

Recreational fisheries landing statistics are collected as part of the NMFS Marine Recreational Fisheries Statistical Survey (MRFSS) program. Port-based samplers conduct intercept interviews with fishermen returning from a day of fishing at sea. These data are supplemented with telephone surveys to estimate total catch and effort as a percentage of population size and the catch of those fishermen identified.

Surveys and Fishery Independent Data

NMFS and state agencies also collect and analyze data on fishery resources independent of the recreational and commercial harvesting sectors. NMFS utilizes a fleet of research vessels operated by the National Oceanographic and Atmospheric Administration (NOAA) to collect this data. Surveys conducted by NMFS range from marine mammal population counts to plankton surveys. The trawl surveys for fish provide an independent index of relative abundance of species taken by the sampling gear, that can be compared to fishery catch per unit effort, also an index of relative abundance. When the two indices together track trends of increasing or decreasing abundance, there is greater confidence in the conclusions drawn from these analyses.

The fishery-independent surveys also provide biological samples for the study of age and growth, mortality, fecundity, etc., in addition to allowing for the collection of oceanographic data that is used to develop ecological models relating fish abundance and distribution to environmental conditions.

Fishery-independent surveys follow a rigorous methodology that is designed to result in statistically valid samples, taken in a consistent and reproducible manner. The protocol for bottom trawl surveys usually follows a random stratified design. The continental shelf water is divided into similar strata by latitude and depth zone, so as to reduce sample variability with strata and therefore increase the precision of abundance estimates. Within strata, station locations are selected randomly, so as to remove possible biases and to meet statistical design requirements. Survey data is used to develop a fishery-independent index of relative abundance (CPUE), so temporal consistency in sampling is extremely important. Considerable effort is expended to ensure that each tow of the trawl is exactly the same as every other tow within each survey, and between past and future surveys. Small changes in sampling method or gear may result in substantial changes in catchability of that gear, so any changes are avoided or investigated thoroughly via paired comparison methods prior to implementation.

Life History Characteristics

Age

The age of some finfish and mollusks can be determined by studying the annual or seasonal marks on the hard parts of the animals, including scales, otoliths, spines or shells (Figure 8). For animals that do not produce body parts that can be used to age the animal, the ages of successive cohorts in a population can be inferred from a multi-modal length-frequency diagram (Figure 9).



Figure 8. Fish scale showing annular growth rings for ages 1 to 4 (Royce 1996).

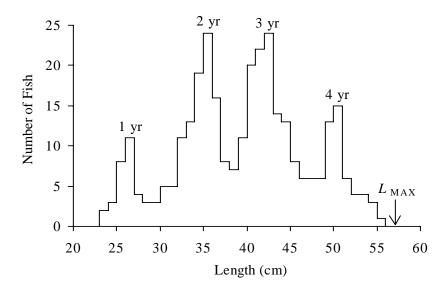


Figure 9. Age determined from multi-modal length frequency plot (Goeden 1978).

Growth

Individual fish growth follows an asymptotic function for both length and weight with respect to time. The growth is continuous, seasonal, or step-wise (in the case of crustaceans that shed their shells or grow in increments). The simplified von Bertalanffy age-length growth equation is:

$$L_{t} = L_{MAX} \left(1 - e^{-Kt} \right)$$

where L_{MAX} is the maximum length of the fish, and K is the instantaneous growth rate.

These characteristics for a large, long-lived fish with L_{MAX} of 100 cm and a K of 0.2 and small, short-lived fish with L_{MAX} of 50 and K of 0.7 are shown in Figure 10.

The weight of a fish is also related to its age using the von Bertalanffy age-weight equation

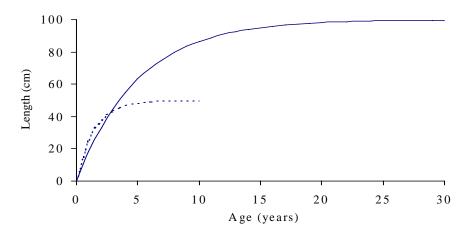


Figure 10. von Bertalanffy age-length relationship for the large, long-lived fish (—) and the small, short-lived fish (- - -).

The relationship between fish weight and length is exponential:

$$W_{t} = aL_{t}^{b}$$

where *a* is the *L-W* conversion coefficient, and *b* is the *L-W* volumetric factor.

The coefficients are a = 0.00001 and b = 3 for the large, long-lived fish, and for the small, short-lived fish are a = 0.00001 and b = 3. The relationship between length and weight is shown in Figure 11, and the relationship between age and weight is shown in Figure 12.

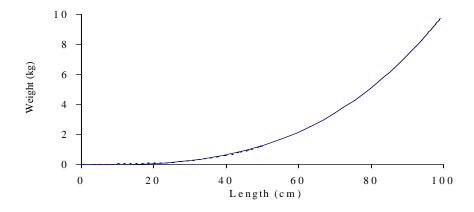


Figure 11. Length-weight relationship for the large, long-lived fish (—) and the small, short-lived fish (- - -).

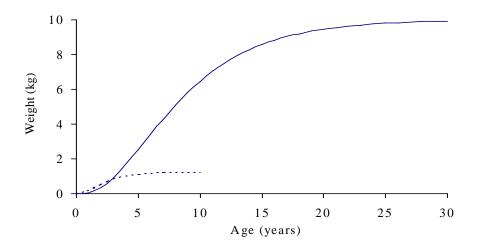


Figure 12. von Bertalanffy age-weight relationship for the large, long-lived fish (—) and the small, short-lived fish (- - -).

Maturity

The sexual maturation of fish occurs as part of the growth and aging process over a period of time. That is, not all fish of the same age (year-class or cohort) mature at the same time. Therefore, the percent maturity of individuals in a cohort at age is described by a logistic function:

$$P_{t} = (1 + e^{-\alpha 1 * (t - \beta 1)})^{-1}$$

where $\alpha 1$ is the steepness of the curve, and $\beta 1$ is the age at 50% maturity.

For the large, long-lived fish, where $\alpha 1 = 1$ and $\beta 1 = 6$ and the small, short-lived fish where $\alpha 1 = 1.5$ and $\beta 1 = 3$, the relationships for percent maturity as a function of age and length are shown in Figures 13 and 14, respectively.

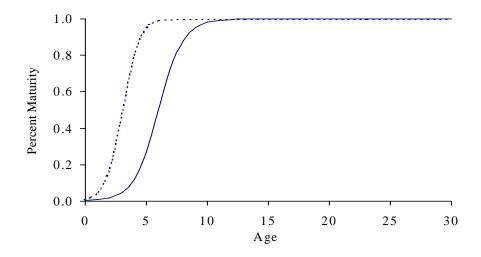


Figure 13. Percent maturity as a function of age for the large, long-lived fish (—) and the small, short-lived fish (- - -).

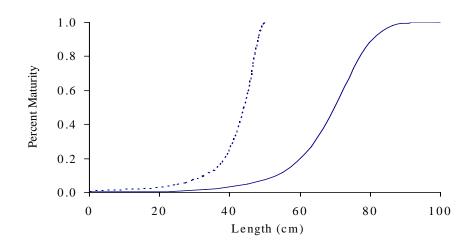


Figure 14. Percent maturity as a function of length for the large, long- lived fish (—) and the small, short-lived fish (- - -).

Mortality

Each year the mature adults in the fish stock spawn and those animals that survive the larval phase recruit to the stock as young of the year (YOY), age 0 individuals. The number of individuals remaining in that cohort is expressed as:

$$N_{t} = N_{0} * e^{-Mt}$$

where N_0 is the number of recruits, and M is the instantaneous natural mortality rate.

For long-lived animals (about 20 years), the instantaneous natural mortality rate is 0.2, and for short-lived animals (about 5 years), the instantaneous natural mortality rate is 0.7.

The instantaneous rate can also be expressed as an annual percentage loss rate where 0.2 and 0.7 are equivalent to 19% and 50% annual loss rates, respectively. A cohort or year-class of animals is considered reduced to non-existent level when the remaining numbers in a cohort are less than 3 to 5% of those recruiting, as shown below for an animal with an instantaneous natural mortality of 0.7 and an arbitrary starting number of 1000 individuals.

Age (year)	Number	Annual Reduction	% Remaining
0	1000	50	100
1	500	50	50
2	250	50	25
3	125	50	12
4	62	50	6
5	31	50	3

For the large, long-lived fish (M = 0.2) and small, short-lived fish (M = 0.7), when N_0 is arbitrarily set at 1000, an exponential decay of cohort numbers is observed (Figure 15).

The biomass (B_t) of the individuals remaining in the unfished cohort-at-age (t) is calculated as:

$$B_t = N_t * W_t$$
.

For the cohort of a large, long-lived and small, short-lived fish, biomass as a function of age and length is shown in Figures 16 and 17, respectively.

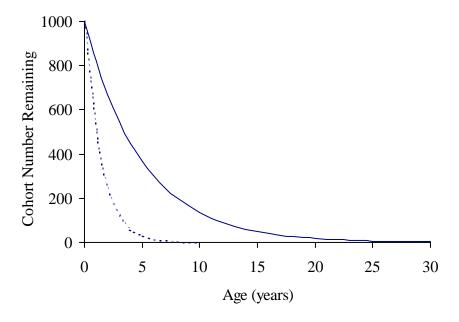


Figure 15. Numbers of an unfished cohort as a function of age for the large, long-lived fish (--) and the small, short-lived fish (---).

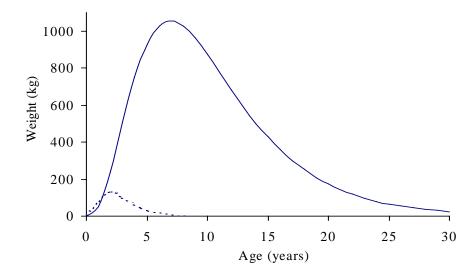


Figure 16. Biomass of the unfished cohort as a function of age for the large, long-lived fish (—) and the small, short-lived fish (- - -).

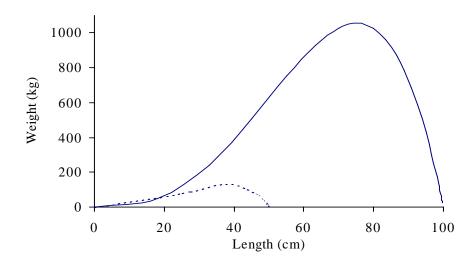


Figure 17. Biomass of the unfished cohort as a function of length for the large, long-lived fish (—) and the small, short-lived fish (- - -).

The unfished spawning stock biomass $(UFSSB_t)$ of the individuals remaining in the cohort-at-age (t) is determined as:

$$UFSSB_{t} = P_{t} * B_{t}$$

and for the unfished cohort, the spawning stock biomass curve is identical to the biomass curve, except that the ascending left side of the curve is shifted to the right slightly to account for young animals that are not mature (Figure 18).

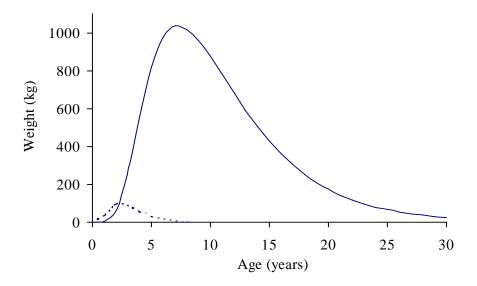


Figure 18. Spawning stock biomass of the unfished cohort as a function of age for the large, long-lived fish (—) and the small, short-lived fish (- - -).

Estimation of Population and Fishing Parameters

Exploitation

Exploitation further reduces the numbers on fish in a stock or a cohort within a stock. The effects of removals due to fishing results in a mortality that is additive to losses due to natural mortality. Fishing mortality is expressed as an instantaneous annual rate (F) or as an annual exploitation rate (F%). Total instantaneous mortality (Z) is the sum of natural mortality (M) and fishing mortality (F). The relationship between Z and total percent annual survival (S%) is:

$$S\% = \frac{N_{t-1}}{N_t} = e^{-Zt}$$

and total percent annual mortality (Z%) is:

$$Z\% = 1 - S\%$$

Total mortality of a given cohort can be estimated by monitoring the reduction in numbers of a given cohort over time. From catch curve analysis (CCA), if the catch of a particular cohort in either a scientific sampling or in a commercial fishery reduces annually by 50%, then the total instantaneous mortality (Z) is 0.7, that is both S% and Z% are 50%. Alternatively, if the stock is composed of multiple annual cohorts of equal size, then, a total mortality can be estimated from a sample of the stock ranked by numbers in each age class. If the natural mortality (M) of that fish species is 0.1 based on longevity, then the fishing mortality (F) is 0.6.

The following table converts between the two values in the range usually applied to fisheries problems.

Z (instantaneous)	Z annual % loss	
0.05	5	
0.1	10	
0.5	40	
1.0	64	
1.5	78	
2.0	87	

For the large, long-lived fish, when N_0 is arbitrarily set at 1000, M = 0.2 and F = 1.0 after age 4, the effect of the addition of fishing mortality to the exponential decay of the cohort numbers is easily observed (Figure 19a). For the small, short-lived fish, when N_0 is arbitrarily set at 1000, M = 0.7 and F = 1.0 after age 2, the effect of the addition of fishing mortality to the exponential decay of the cohort numbers is not as distinct (Figure 19b). Higher or lower values of F will increase or decrease the decay in numbers relative to the unfished case.

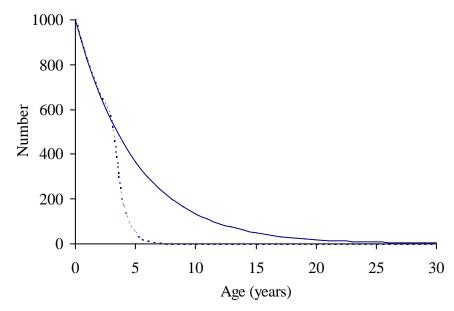


Figure 19a. Numbers an unfished cohort (—) and fished cohort (- - -) as a function of age for the large, long-lived fish.

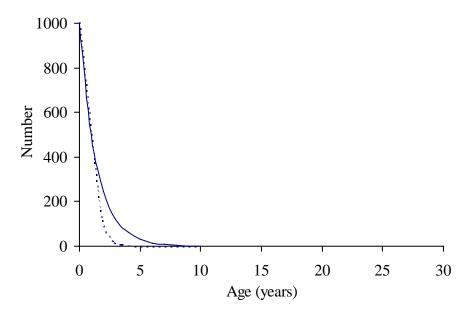


Figure 19b. Numbers an unfished cohort (—) and fished cohort (- - -) as a function of age for the small, short-lived fish.

Harvesting Selectivity

Fishing activity applies a size- or age-specific mortality to the cohort. The size selection characteristics of the gear can follow either a sigmoid curve that is represented by a logistic cumulative distribution function (LCDF) or a dome-shaped curve that is represented by a rescaled normal probability density function (NPDF).

Trawl codend and longline hook size selection may be modeled by a LCDF. Small fishes are not captured by the gear as they either pass through the meshes of a net or can not take a hook due to their small mouth size; large fish are retained by the net meshes and are captured by the hooks. The probability of selection for an individual fish of length (L) is:

$$PL_{L} = (1 + e^{(-\alpha 2*(L-L_{50}))})^{-1}$$

where $\alpha 2$ is steepness of the curve, and L_{50} is length at 50% selection.

For the large, long-lived fish, if steepness is set at 0.33, then a series of curves for L_{50} s of 50 to 100 cm can be described as in Figure 20. Each curve represents the catch characteristics of a single mesh or hook size.

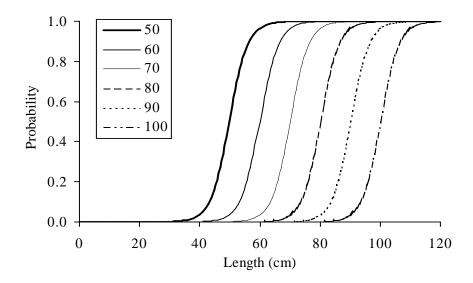


Figure 20. LCDF size-selection curves.

Gillnet and trap/pot size selection may be modeled by a NPDF. With regard to the gillnet, neither small or large fish are taken by the mesh of a particular size. For the trap, retention of small fish is regulated by outer wall mesh size and large fish are restricted from entering the trap by the size of the funnel opening. The probability of selection for an individual of length (L) is:

$$PN_{L} = e^{\left[-(L-L_{opt})^{2}/(2*SD^{2})\right]}$$

where SD is the standard deviation, and L_{opt} is the length at optimum selection.

For the large, long-lived fish, if the standard deviation is set at 5, then a series of curves for L_{opt} s of 50 to 100 cm can be described as in Figure 21. Each curve represents the catch characteristics of a single gillnet mesh size, or trap mesh size and funnel diameter.

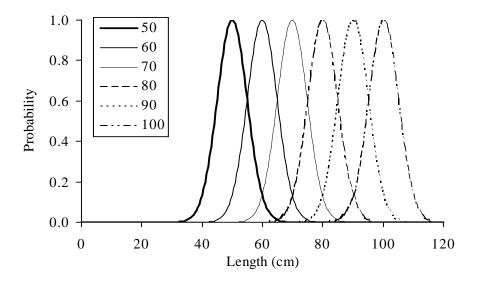


Figure 21. NPDF size-selection curves.

Fishing mortality removes animals from the stock and is expressed as an instantaneous rate (F), similar to natural mortality (M). However, the vulnerability to harvesting activity is controlled to the size selectivity of the gear, so fishing mortality is applied to a cohort as the product of F and PL_L or PN_L . That is, small fish are not susceptible to the gear, are not harvested by the gear, and therefore do not contribute to fishing mortality. Thus, the number of fish remaining in a cohort is expressed as:

$$N_{t} = N_{t-1} e^{-(F*(PL_{L}orPN_{L})+M)t} = N_{t-1} e^{-(Z)t}$$
.

Yield per Recruit and Other Dynamic Pool Models

Yield-per-recruit (YPR) models are useful to fishery resource managers for predicting the effects of alterations in harvesting activity on the yield available from a given year-class or cohort. Two elements that define the model and are usually regulated by resource managers are fishing mortality (*F*) and the pattern of harvesting activity on different sizes of fish. Often the latter element has been simplified by assuming knife-edge selection (100% vulnerability at age of first capture). The Beverton and Holt analytical solution to the yield equation was initially developed to estimate YPR. While the knife-edge selection assumption may be appropriate for size selection that follows a logistic distribution function, as is observed in a trawl codend, the Beverton-Holt yield equation does not incorporate recent advances in understanding the size selection processes of the principal gear types used on groundfish (trawls, traps, gillnets, and longlines).

To predict the yield from a given number of recruits in a single cohort of fish, parameters characterizing the life history of the fish species and affecting the harvest of the stock must be specified. While the life history parameters affect the potential biomass available from the cohort, harvest related factors are controlled by fisheries management and ultimately affect the yield taken from the biomass. The biological or life-history parameters affecting the potential maximum biomass and the timing of the maximization are:

K is the instantaneous growth rate, M is the instantaneous natural mortality rate, W_{∞} is the maximum weight of an individual fish.

The fishery related factors affecting the maximum potential yield are:

 t_c is the age at which fish enter the fishery, controlled by mesh size in a trawl fishery,

F is the instantaneous fishing mortality rate.

Beverton and Holt noted several important results from the yield per recruit analysis. Most important is the ratio of the growth parameter (K) to the natural mortality coefficient (M), which estimates the potential of a fish to complete its potential growth before dying of natural mortality.

If M/K is small (M/K < 0.5), then growth is high relative to mortality, and the cohort will reach maximum biomass at a larger size relative to the maximum size, or the stock (in the absence of fishing) will contain relatively larger fish. From a fishery perspective, management should maximize the size or age of entry to the fishery (t_c) with minimal fishing mortality on smaller fish.

If M/K is large (M/K > 1.5), then natural mortality exceeds growth, indicating many fish will die before completing their potential growth. Again, from a fishery perspective, management should allow heavy fishing with a small size (early age) at first capture, so as to harvest the maximum biomass before they die of natural causes.

Essentially, as the M/K ratio increases, the peak of the unfished cohort biomass curve (Figure 22) shifts to the left, suggesting that the age or length at which harvesting pressure should be applied is a smaller value.

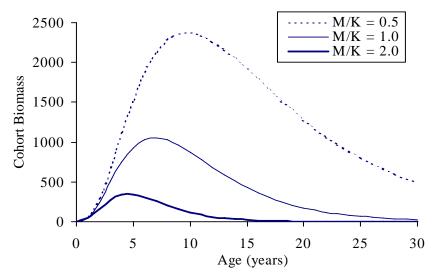


Figure 22. Effect of mortality rate on cohort biomass given a fixed growth rate.

The yield-per-recruit (YPR) analysis generates a function that describes the relationship between yield and fishing mortality for the specific biological parameters that describe the life history of the animal, and the fishery parameter that describes the age or size of entry into the fishery based on gear selectivity (Figure 23). At F = 0, there is obviously no yield, and as F increases, yield increases rapidly, reaching a maximum value (F_{MAX}), then either declines with increasing F or asymptotes, depending on the age or size of entry into the fishery. Harvesting at fishing mortality rates greater than F_{MAX} is not productive as it results in declining yield.

The corollary to the YPR analysis is the spawning stock biomass per recruit (SSBPR) analysis. In this case, the biomass of mature animals remaining in the cohort are determined after extracting the yield, and the animals are valued for their contribution to future recruitment for the stock. The SSBPR analysis generates a function that describes the relationship between spawning stock biomass and fishing mortality (Figure 23). At F = 0, the SSBPR value is at a maximum (unfished SSB), as there is no harvesting, and from there it declines sharply as F

increases, finally approaching a minimum value at the highest F levels. The reference point $F_{20\%SSB}$ refers to the level of fishing mortality that retains 20% of the SSB at F=0.

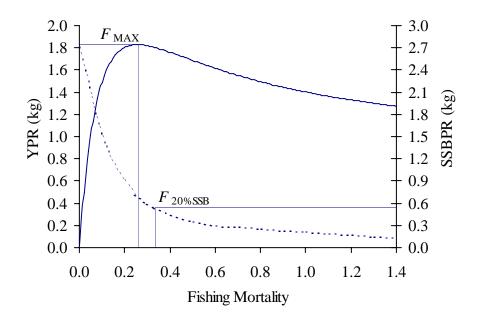


Figure 23. Yield per recruit (YPR) (—) and spawning stock biomass per recruit (SSBPR) (- - -) relationship.

Recruitment

Recruitment processes include those factors affecting the growth and survival of the fish between the egg and age that the fish enters either the spawning stock biomass portion of the population or becomes vulnerable to harvesting. The purpose of investigating stock-recruitment relationships for fishery resource stocks is to be able to predict the number of recruits to the fishery at a future date based on estimates of the present spawning stock abundance. Alternatively, using a stock-recruitment relationship, resource managers can regulate fishing mortality levels so as to avoid low stock levels that would result in recruitment failure. This latter process is referred to as recruitment overfishing, and is controlled using a fishing mortality reference point related to SSBPR, $F_{20\%SSBPR}$.

Recruitment can be measured at any point in the life history of the fish, and expressed as numbers or biomass. Recruitment indices track individual year-classes from age 0 on. Both density-dependent and density-independent mortality affect the fish survival, especially in the early life history stages. Environmental factors are especially important in this latter category.

The stock-recruitment relationship has some basic tenets:

- 1. The stock-recruitment function must pass through the origin, that is, at $S(0) \rightarrow R(0)$.
- 2. At any stock levels beyond S(0), R > 0.
- 3. The rate of recruitment (R/S) should decrease continuously with increasing S.

4. Recruitment (*R*) must exceed parental stock size (*S*) over some range of (*S*) (when *R* and *S* are in the same units), otherwise stock collapse would result from any perturbation to the system.

There are two basic stock-recruitment relationships widely referred to in the fisheries literature. Both relationships include density-dependent processes that limit recruitment at large stock size. The Beverton-Holt relationship is characterized by a curve with a slope that continues to decline as the curve approaches an asymptote (Figure 24). The general form of the relationship is:

$$R = \frac{1}{(\alpha + \beta/S)}$$

where R is recruitment numbers, S is stock number, and α and β are constants.

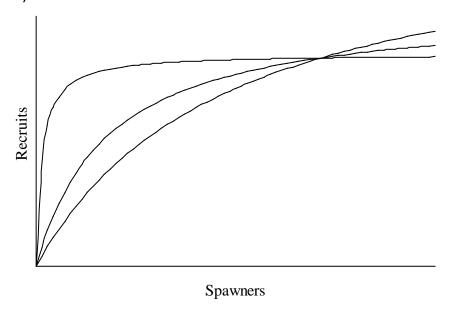


Figure 24. Beverton-Holt stock-recruitment relationships.

The Ricker relationship is characterized by a curve that declines at high stock levels (Figure 25). The general form of the relationship is:

$$R = \alpha S e^{-\beta S}$$

where R is recruit number, S is stock number, α is a constant; slope at the origin, and β is a constant; shape of the curve.

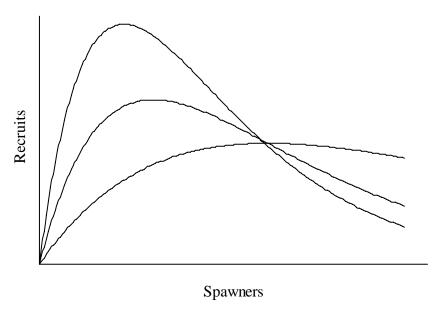


Figure 25. Ricker stock-recruitment relationships.

In general, marine species' stock recruitment relationships are best represented by the Beverton-Holt curves, and anadromous and fresh water species are best represented by the Ricker curve.

Production Models

Production models consider a population of fish as a single unit of biomass subject to constant growth and mortality rates. In contrast, dynamic pool and cohort models consider growth, mortality, and reproduction as a function of age, size, or groups of ages and sizes. The production models are based on density-dependent processes for birth or death, that is, as population size increases, death rate increases, and birth rate decreases. The processes combine to result in a logistic model for population size over time that asymptotes at the carrying capacity of the environment (K) (Figure 26). The derivative or slope of the population size function over time is parabolic; a dome-shaped function that is a measure of the production potential of the stock (Figure 27), which is described by the Schaefer model:

$$\frac{dB}{dt} = rB\left(1 - \left(\frac{B}{k}\right)\right) - C$$

where *r* is the intrinsic population growth rate, *B* is the biomass of the stock, *k* is the carrying capacity, and *C* is the catch rate.

Note that this function reaches a maximum at one-half the maximum population size or one-half the carrying capacity of the environment for this stock.

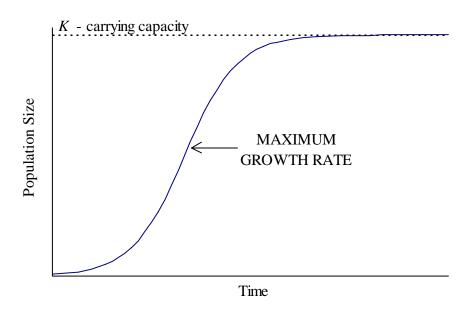


Figure 26. Logistic model for population size as a function of time.

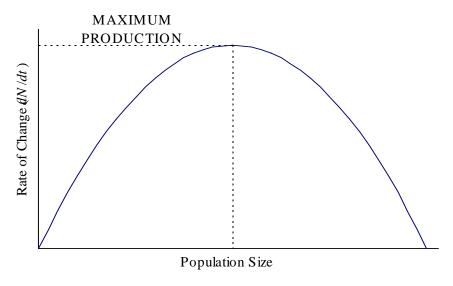


Figure 27. Rate of change in population size as a function of population size.

The excess production potential can be removed from the population as yield and the population size will remain stable. Therefore, the potential sustainable yield of a stock is related to population size (Figure 28). The function is a dome-shaped function, where sustainable yield is 0 at the minimum and maximum population levels, and is maximized (maximum sustainable yield (MSY)) at one-half maximum population size.

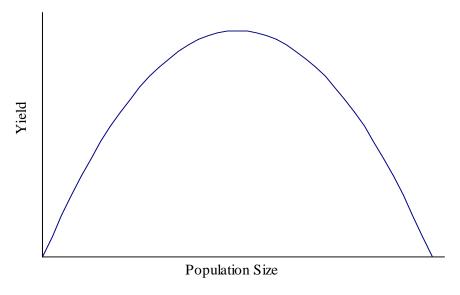


Figure 28. Equilibrium yield as a function of population size.

The sustainable yield available from a fishery stock unit is referred to as the surplus production. Using the surplus production model, equilibrium yield is related to fishing mortality or fishing effort at an equilibrium biomass level, again with a dome-shaped function (Figure 29). Similarly, at minimum and maximum effort, equilibrium yield approaches 0 and the optimum fishing mortality rate or effort is one-half the maximum value, thereby providing the maximum equilibrium yield (MEY) at that population level.

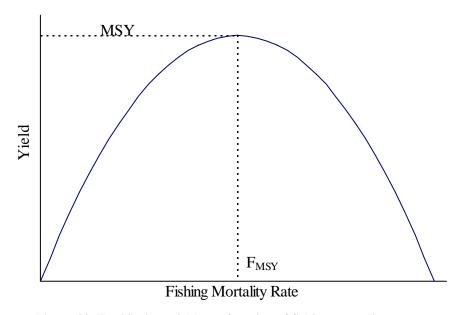


Figure 29. Equilibrium yield as a function of fishing mortality rate.

From a management perspective, it is desirable to attempt to manage the biomass level so as to produce MSY, and to manage the fishing mortality rate at that biomass level so as to produce the MEY.

Indices of Stock Abundance

The past, present, and future status of a stock of fish is usually measured or expressed as an index of abundance. Those temporal indices are either relative or absolute, reflect numbers or biomass, and can be partitioned by sex, juvenile vs. adult, etc. The relative indices are based on catch per unit effort (CPUE) data from fishery independent or dependent sources. For example, a time series of CPUE in numbers for a standardized seine survey in upper Chesapeake Bay provides a relative index of abundance of Young of the Year (YOY) striped bass in a major nursery area. Similarly, a CPUE time series from a commercial trawl fishery for flounder provides a relative index of abundance for adult fish available to the fishery. Trends in these relative indices of abundance are used to predict the future status of a resources. A positive trend in the YOY striped bass index suggests an increase in recruitment to the fishery in the future, while a negative trend in an adult relative index of abundance may be indicative of overfishing and a declining resource. Long-term indexes of relative abundance are very useful to study cyclic patterns in abundance that can be related to interactions with other species, an environmental variability, and most importantly are required input to most stock assessment models that estimate absolute indices of abundance.

Absolute indices of abundance for various components of a stock can be estimated from the analysis of catch at age data from either the fishery or scientific surveys using sequential age analysis. Virtual population analysis or cohort analysis are methods that utilize catch at age data to estimate both fishing mortality rates and cohort number. A matrix of annual catch at age data is used to develop a matrix of cohort number at age data, that is then used to estimate the stock structure, number by cohort available in each year. With a knowledge of past and present stock structure, the effects of alternative management strategies on the stock can be determined.

Fisheries Management

The Magnuson Fishery Conservation and Management Act, enacted in 1976, empowered the federal government to regulate fishing from 3 to 200 miles off the coasts of the United States. The Act created eight regional fishery management councils that are charged with the responsibility of developing fishery management plans (FMPs) for stocks within their region. Council members include representatives from each state who then represent the regulatory, recreational, commercial, and conservation constituencies. Each council has an executive director and staff to assist in the preparation of FMPs.

NMFS is mandated by Congress to collect and analyze data on the status of the fishery resources off the coasts of the United States and on the fisheries. NMFS then provides this information to the management councils for their use.

Additionally, the councils have committees and panels that provide further technical assistance to the council staff and members on scientific and sociological issues related to the FMPs. Rules for the development of FMPs are referred to as the 602 guidelines, and provide directions for the definition of overfishing, the establishment of measures to prevent overfishing, and the development of a program for rebuilding a stock if overfishing already exists. Public input and comment is sought throughout the FMP development process. FMPs are modified through plan

amendments that also allow for public input and comment. However, if conditions in the fishery are changing rapidly, framework action notices are used to allow management to keep pace with an evolving fishery.

The original Magnuson Act and the recently re-authorized Magnuson-Stevens Act provide national standards for the management of fishery resources. The standards promote conservation and utilization of the fishery resources based on the best scientific information available, seek to promote optimum sustainable yield while preventing overfishing, protect the habitats for fishery resources, etc.

After the fishery management plan amendment or notice action has proceeded through the regulatory process, it is published in the federal register. Management measures become federal regulations and these are enforced by NMFS law enforcement agencies, the U.S. Coast Guard, and others. Violations are subject to civil and criminal sanctions. Civil sanctions include written warnings, fines issued by Notices of Violations and Assessment (NOVA), forfeiture of seized property including catch, vessels, and equipment, and finally, permit sanctions.

In addition to the regional management councils, there are three regional interstate fishery management commissions established by federal law: the Atlantic States Marine Fisheries Commission (ASMFC), the Gulf States Marine Fisheries Commission, and the Pacific States Marine Fisheries Commission. These commissions include three representatives from each state in the region, again representing various constituencies. These commissions were charged by Congress to promote and encourage management of interjurisdictional marine resources. The Atlantic Coastal Fisheries Cooperation Management Act passed by Congress in 1993 charged the ASMFC with the responsibility of developing FMPs for transboundary, migratory coastal species.

Management strategies for controlling harvest rates include restricting effort, catch quotas, closed areas, etc. U.S. fisheries have traditionally been open-entry or open-access fisheries. Since the passage of the Magnuson Act, there has been steady growth in the harvesting capacity. Thus, as we enter the twenty-first century, there is excess capacity or over-capitalization in our fisheries, resulting in overfishing of limited resources. To limit or restrict overfishing, management has responded in some fisheries by issuing seasonal or annual total allowable catch (TAC) regulations. These quotas result in "derby fisheries" where individual fishermen attempt to catch as much as they can, until the quota is reached and the fishery closed. These derbies result in temporary market gluts and lower prices paid for catch to fishermen. Other methods to control fishing mortality include limiting effort by closing fishing areas during specific times to protect spawning aggregation of fish or nursery areas, allowing vessels only limited number of days at sea, restricting the vessel size, horsepower, or the amount of gear fished.

The most controversial effort-control measure, however, is limited entry. This is a fundamental change in the traditional open-access fishery management policy in the U.S. Limited entry begins with a moratorium on new licenses. A related issue is the transferability of licenses, i.e., can an individual sell his license, or can potential new entrants to the fishery apply to a lottery to enter the fishery, as existing participants leave the fishery.

Another aspect of limited entry is the provision for property rights through individual transferable quotas (ITQ) or sector quotas. In individual quota fisheries, access to the fishery is controlled with a moratorium on new licenses, then fishermen are individually awarded a portion or allocation of the total allowable catch (TAC) each year, and that share may be transferable to other fishermen via direct sale. Thus larger, more efficient harvesters are able to purchase the shares of the smaller, less efficient harvesters. This results in consolidation of harvesting capacity and increased economies of scale. Typically, limits are placed on the total number of shares an individual or corporation may acquire so as to avoid monopoly situations. With the establishment of sectors that are provided "catch shares", groups of fishermen are provided a portion of the TAC, and the group of fishermen cooperatively work together to allocate individual portions of their TAC,

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Chapter II

MATHEMATICS AND BIOSTATISTICS REVIEW

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Note: This chapter is adapted from materials presented in Chapter 2 of Gulland (1969) and Chapter 2 of Sparre *et al.* (1989). Additional references are provided at the end of the chapter.

Functions

If to each value of x there corresponds one or more values of a variable y, then y is a function of x, and we write y = f(x) where f symbolizes the function (Figure 1). The relation y = f(x) is defined as a continuous set of points forming a line or curve. Note the ordinate or y-axis evaluates the dependent variable y, and the abscissa or x-axis evaluates the independent variable x.

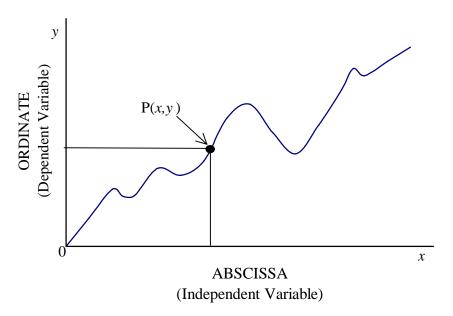


Figure 1. Function: y = f(x).

A linear function can be described by:

$$y = ax + b$$
,

where a and b are constants (Figure 2).

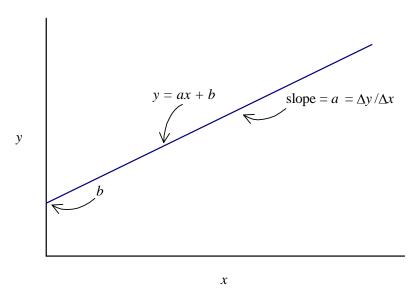


Figure 2. Linear function: y = ax + b.

The slope of the line is a and the y-axis intercept is b. The slope is defined as the change in y divided by the change in x. Mathematically, this is expressed as $\frac{\Delta y}{\Delta x}$ or $\frac{dy}{dx}$. Special cases of the linear function occur when b = 0 (y = ax; i.e., the function intersects the origin), (Figure 3a) and when a = 1 and b = 0 (y = x) (Figure 3b).

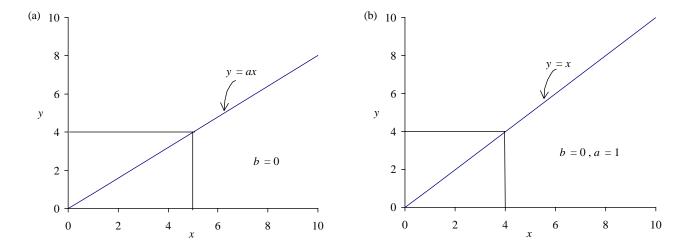


Figure 3. Special cases of linear functions:

- (a) y = ax
- **(b)** y = x.

Note the effect of value of the slope a on the linear function (Figure 4). The function trends upward if a > 0, is a horizontal line parallel to the abscissa if a = 0, and trends downward if a < 0.

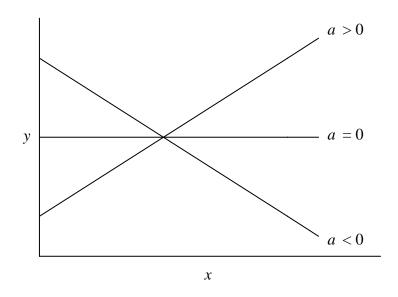


Figure 4. Effect of the slope a on the linear function.

A more complex function is the second order polynomial, or quadratic function described by

$$y = ax^{2} + bx + c$$
or
$$y = A(x - x_{0})(x - x_{1})$$

where x_0 and x_1 are x-axis intercepts and A determines whether the curve is concave upward or downward (Figure 5).

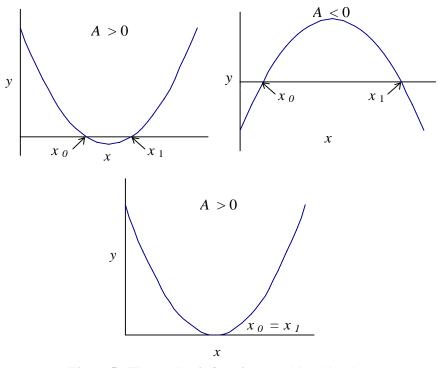


Figure 5. The quadratic function: $y = A(x-x_0)(x-x_1)$.

The parabola is a special case of the second order polynomial, where A < 0, $x_0 = 0$, and $x_1 = b$ (Figure 6).

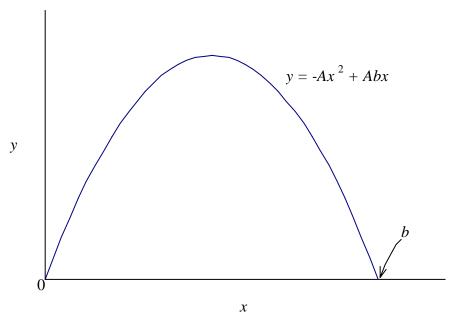


Figure 6. Parabola: $y = -Ax^2 + Abx$.

An exponential function is described by

$$y = a^x$$

where a is a constant raised to an exponential power, x (Figure 7). As with the linear function, x is the independent variable, and y is the dependent variable.

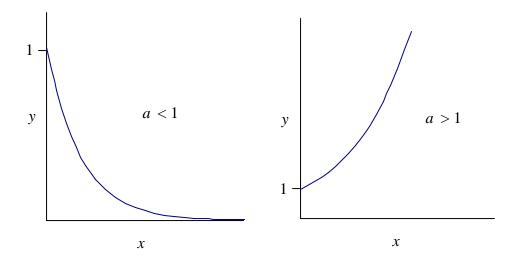


Figure 7. Exponential functions: $y = a^x$.

The exponential function increases to infinity if a > 1. The function decreases asymptotically and approaches the *x*-axis if a < 1. An asymptotic function is described by a curve that approaches a singular value on the *y*-axis as the values on the *x*-axis become larger and larger.

Another example of an asymptotic function is

$$y = 1 - e^{-x}$$

where the function approaches y = 1 as x increases in value (Figure 8).

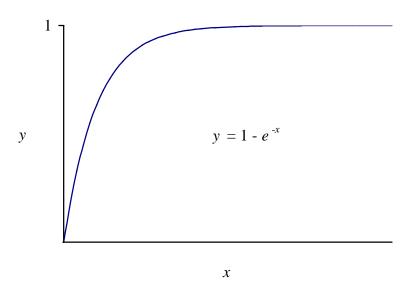


Figure 8. Asymptotic function: $y = 1 - e^{-x}$.

A power function is described by

$$y = x^N$$

where *N* is a constant (Figure 9).

If N > 1, then the curve ascends rapidly. If N = 1, then y = x is a straight line. If N < 1, then the curve ascends slowly.

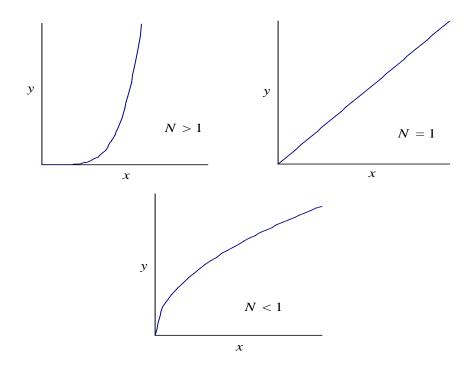


Figure 9. Power functions: $y = x^N$.

Powers and Logarithms

A power is represented by two numbers and is expressed as a^N , where a is the base and N is the exponent. The following laws apply to powers:

$$a^{0} = 1$$

$$a^{-M} = \frac{1}{a^{M}}$$

$$(a^{N}) \cdot (a^{M}) = a^{(N+M)}$$

$$(a^{N})/(a^{M}) = a^{(N-M)}$$

$$(a^{M}) \cdot (b^{M}) = (a \cdot b)^{M}$$

$$(a^{M})/(b^{M}) = (\frac{a}{b})^{M}$$

$$(a^{N})^{M} = a^{NM}$$

$$a^{M/N} = \sqrt[N]{a^{M}}$$

The inverse function of a power is a root, and the inverse function of an exponential is a logarithm. For example, consider the exponential function

$$y = a^x$$
.

Taking the logarithm to the base a of both sides of the equation yields

$$\log_a y = x(\log_a a) = x(1)$$
or
$$x = \log_a y.$$

The bases most commonly used for logs are 2, 10, and e where $e \approx 2.72$. Log base $2(\log_2)$ is the basis of binary algebra; base $10(\log_{10})$ is the basis of the numerical system; and base $e(\log_e)$ is the basis of the Napierian system.

Log_e is referred to as the natural log and can be abbreviated as "ln." The natural log has convenient properties in calculus, and the value of *e* is described by

$$e = \lim_{h \to \infty} \left(1 + \frac{1}{h} \right)^{h}$$

= 1 + $\left(\frac{1}{1!} \right)$ + $\left(\frac{1}{2!} \right)$ + $\left(\frac{1}{3!} \right)$ + ... = 2.7182

where "!" indicates "factorial" (i.e., a series product of descending integers); for example,

$$4! = (4)(3)(2)(1) = 24.$$

The following laws apply to logarithms:

$$\log_{10} 10 = 1$$

$$\log_{e} e = \ln e = 1$$

$$\log_{10} 1 = \ln 1 = 0$$

$$\log_{a}(x) + \log_{a}(y) = \log_{a}(x \cdot y)$$

$$\log_{a}(x) - \log_{a}(y) = \log_{a}\left(\frac{x}{y}\right)$$

$$\log_{a}(x^{M}) = M \log_{a}(x).$$

Transforming or Linearizing Functions

Non-linear functions can sometimes be simplified for evaluation or fitting models by transforming or linearizing the function. Consider the negative exponential, which is frequently used in population dynamics to describe the survival of animals in a stock as a function of time, and a specified mortality coefficient. The function, shown in Figure 10a, has the form:

$$y = Ae^{-zx}.$$

The estimation of parameters A and z from (x, y) data points requires non-linear regression techniques that until recently were not readily available. However, a linear function can be

obtained by transforming the original function using natural logarithms. This simplified function (Figure 10b) can be analyzed using linear regression techniques:

$$\ln y = \ln A - zx \ln e$$
$$= \ln A - zx$$

which is in the linear form of

$$y = b - ax$$
.

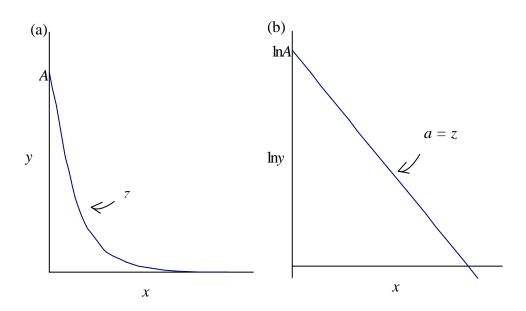


Figure 10. Non-linear and linear forms of $y = Ae^{-zx}$.

The parameter A is obtained by taking the inverse natural log of the y-intercept (b) in the linearized form. The parameter z is obtained directly from the slope a in the linearized form.

A parabolic or dome shaped function is also frequently used in population dynamics to describe the relationship between yield and effort or yield and stock biomass. The general form of the function is:

$$y = bx - ax^2$$

(Figure 11a). Estimation of parameters a and b from (x, y) data points requires non-linear regression techniques. However, transforming the function by dividing both sides of the equation by x, results in the linear form

$$\frac{y}{x} = b - ax$$

(Figure 11b). This form is amenable to simplified regression techniques. The difficulty with this methodology, however, is that the dependent variable (y) has been confounded with the presence of the independent variable (x).

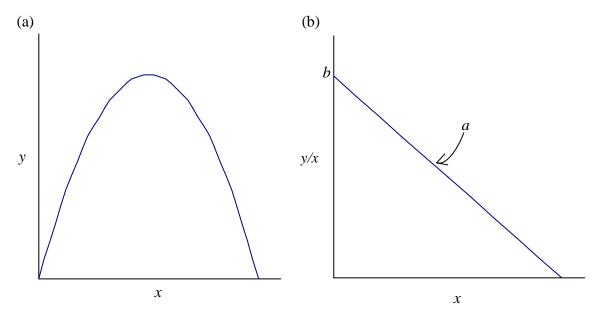


Figure 11. Non-linear and linear forms of $y = bx - ax^2$.

Differential Calculus

Differential calculus is concerned with rates of change. We often refer to a derivative which is a function that measures the rate of change of a quantity. For example, a derivative function may indicate how fast *y* changes with respect to *x* at any point x (*i.e.*, the instantaneous slope) (Figure 12). The derivative is indicated by:

$$\frac{dy}{dx}$$
 or $y' = f'(x)$.

The slope or derivative of a linear function (*i.e.*, a straight line) is a constant. However, for a parabolic function, the slope is initially positive, decreases to zero at the apex of the parabola, and becomes increasingly negative as it approaches the *x*-axis intercept.

The following are functions and their derivatives:

Function	Derivative
a (constant)	0
ax	a
ax^N	aNx^{N-1}
lnx	$\frac{1}{x}$

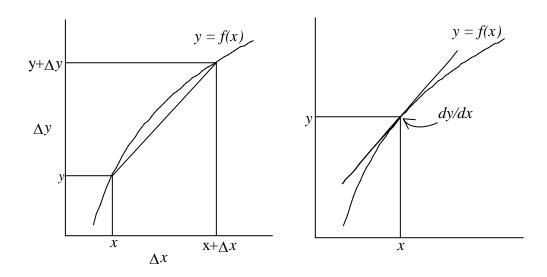


Figure 12. Derivative of the function y = f(x).

Examples of differential calculus are the following:

$$\frac{d}{dx}(x) = 1$$

$$\frac{d}{dx}(3x) = 3$$

$$\frac{d}{dx}(3x+2) = 3+0=3$$

$$\frac{d}{dx}(3x^2) = 3 \cdot 2x^{2-1} = 6x$$

$$\frac{d}{dx}(3x \cdot x) = (3x \cdot 1) + (3 \cdot x) = 6x$$

Example 1: Given the parabolic function,

$$y = bx - ax^2$$

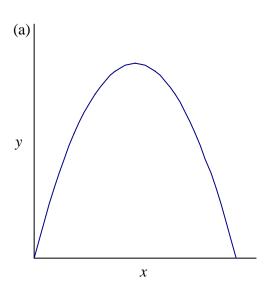
find the x and y values for the maximum of the function (Figure 13a).

Solution: Given the shape of a parabola, the function is at a maximum when the slope = 0. Take the derivative of the function and set it equal to zero (Figure 13b),

$$\frac{dy}{dx} = y' = b - 2ax = 0$$

$$b = 2ax$$

$$x = \frac{b}{2a} .$$



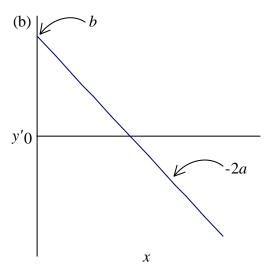


Figure 13. Functions: (a) $y = bx - ax^2$ (b) y' = b - 2ax.

Substituting this value of x into the original function to determine the y-max value,

$$y = b(b/2a) - a(b/2a)^{2}$$

$$y = b^{2}/2a - ab^{2}/4a^{2}$$

$$y = 2b^{2}/4a - b^{2}/4a = b^{2}/4a$$
.

Thus, the coordinates of the y-max for the parabolic function are:

$$x = \frac{b}{2a}$$
$$y = \frac{b^2}{4a} .$$

Integral Calculus

Integral calculus is concerned with summing quantities that are changing and can be thought of as the inverse of differentiation (*i.e.*, the anti-derivative). An integral can be definite or indefinite. The definite integral is conceptually equivalent to the area under a curve and between specified limits a and b on the curve or function. The area bound by the curve y = f(x), the x-axis, the lower bound x = a, and the upper bound x = b (Figure 14). The definite integral of f(x) between a and b is indicated by:

$$\int_{x=a}^{b} f(x) dx$$

where f(x)dx is the integral and [a, b] is the range of integration.

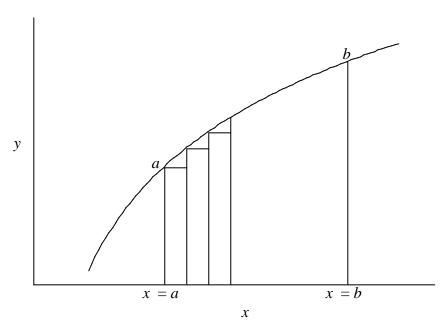


Figure 14. The integral of a function: y = f(x).

It follows that the solution to the definite integral of f(x) between a and b is:

$$\int f(x)dx = \left[F(x)\right]_a^b = F(b) - F(a)$$

where F(x) is a function such that F'(x) = f(x) for x = a and b.

An indefinite integral is a function F(x) such that F'(x) = f(x) (i.e., F(x) is the anti-derivative of f(x)). F(x) + c, where c is a constant, is also an indefinite integral of f(x) because [F(x) + c]' = F(x) = f(x).

The following are some rules of integration:

$$\int adx = ax$$

$$\int af(x)dx = a \int f(x)dx$$

$$\int x^{M} dx = \frac{x^{(M+1)}}{(M+1)} \qquad M \neq -1$$

$$\int a^{x} dx = \frac{a^{x}}{\ln(a)} \qquad a > 0, a \neq 1$$

$$\int e^{x} = e^{x}$$

$$\int e^{ax} = \frac{e^{ax}}{a}$$

$$\int \frac{1}{x} dx = \ln(x)$$

$$\int \ln(x) dx = x \ln(x) - x$$

$$\int [f(x) + g(x)] dx = \int f(x)g'(x) - \int g(x)f'(x)$$

$$\int f(x)g'(x) = f(x)g(x) - \int f'(x)g(x) dx$$

Example 2: Determine the area under the function

$$y = 3x^2 + 5$$

for x = 2 to 4.

Solution:

The equation $y = 3x^2 + 5$ is a power function that intersects the y-axis at a value of 5.

The integral of the function is:

$$\frac{dy}{dx} = 3x^{2} + 5$$

$$dy = (3x^{2} + 5)dx$$

$$\int_{2}^{4} dy = \int_{2}^{4} \left[x^{3} + 5x \right] dx = \left[x^{3} + 5x \right]_{2}^{4}$$

$$= (64 + 20) - (8 + 10)$$

$$= 66.$$

That is, the area under the curve $y = 3x^2 + 5$ between x values of 2 and 4 is 66.

Differential Equations

A differential equation is a function that includes a derivative. Conceptually, it is an equation that includes one variable that changes with respect to another variable:

$$\frac{dy}{dx} = f(x)$$
 or $\frac{dy}{dx} = ay$.

Typically, differential equations are used to describe rate processes, such as the decay of radioactive materials or the decline in population numbers as a function of stock size. The decline in population numbers as a function of stock size is described by:

$$\frac{dN}{dt} = -ZN$$

where N is the population size,

Z is the mortality rate, and

 $\frac{dN}{dt}$ is the rate of change of the population size over time.

The equation states that the rate of change of population size is equal to the product of the instantaneous mortality coefficient and the population size.

Solving differential equations is generally complex, but there are some simple solution techniques. The rate equation is solved by the separation of variables technique. The generalized rate equation is:

$$\frac{dy}{dx} = ay.$$

Rearranging and separating variables:

$$\int_{y}^{\infty} dy = adx.$$

Integrating both sides of the equation:

$$\int \frac{1}{y} dy = \int a dx$$

$$\ln y \Big|_{y_0}^{y_x} = ax \Big|_{0}^{x}.$$

Evaluating the integrals and rearranging:

$$\ln(y_x) - \ln(y_0) = ax - a * 0$$

$$\ln(y_x) - \ln(y_0) = ax$$

$$\ln\left(\frac{y_x}{y_0}\right) = ax$$

$$\frac{y_x}{y_0} = e^{ax}$$

$$y_x = y_0 e^{ax}.$$

Applying this solution technique to the population rate equation:

$$\frac{dN}{dt} = -ZN$$

$$\frac{1}{N}dN = -Zdt$$

$$\int \frac{1}{N}dN = \int -Zdt$$

$$\ln N \Big|_{N_0}^{N_t} = -Zt \Big|_{0}^{t}$$

$$\ln(N_t) - \ln(N_0) = \ln(N_t / N_0) = -(Z * t - Z * 0)$$

$$N_t = N_0 e^{-Zt}.$$

Thus the solution to the rate differential equation is the exponential decay equation. Therefore, we use differential equations to find the value of a quantity (e.g., population size N) when we know how fast it is changing (e.g., $\frac{dN}{dt}$). Note that the derivative of this equation $\binom{d}{dt}$ provides the original differential equation

$$\frac{d}{dt}(N_{t}) = \frac{d}{dt}(N_{0}e^{-Zt})$$

$$\frac{dN_{t}}{dt} = N_{0}e^{-Zt}(-Z).$$
Substituting
$$N_{0} = N_{t}e^{Zt}$$

$$\frac{dN_{t}}{dt} = N_{t}(-Z)$$

$$\frac{dN_{t}}{dt} = -ZN.$$

Descriptive Statistics

Statistics can be used to describe the properties of a set of data. Descriptive statistics are used to characterize the central tendencies of the data and the variability around those central measures. If the data are a random sample from a large population, the descriptive statistics of the data set can be used to make inference to the properties of the population sampled.

The mean, median, and mode are used to describe the central tendencies of the data. The mean (\bar{x}) is calculated as follows:

$$\overline{x} = \frac{1}{n} \sum_{i=1}^{n} x_i$$

where x_i are individual values in the data, and n is the number of data points.

The median is the value half way between extremes in a ranked data set (*i.e.*, 50% of the values are less than and 50% are greater than the median value). The mode is the data point with the greatest number of observations.

Measures of the variability in the data include the following:

Estimated Variance:
$$s^2 = \left(\frac{1}{(n-1)}\right) \sum_{i=1}^{n} (x_i - \overline{x})^2$$

Standard Deviation:
$$s = \sqrt{\frac{\sum_{i=1}^{n} (x_i - \overline{x})^2}{n-1}}$$

Standard Error:
$$S.E. = \sqrt[S]{\sqrt{n}}$$
.

The Coefficient of Variation (C.V.) is a measure of variability relative to the mean

$$C.V. = \sqrt[S]{\overline{\chi}}$$
.

Example 3: Consider a sample of 20 measures of fork length (cm) for fish taken from a RI salt pond.

15.5	18.2
16.3	19.3
18.3	17.9
17.3	16.5
15.8	20.4
14.9	17.8
16.7	19.7
17.3	18.4
16.2	18.6
17.8	17.4

Calculating the descriptive statistics provides:

Sample size = n = 20

Mean =
$$\overline{x}$$
 = 17.5 cm

Variance =
$$s^2 = 2.0 \text{ cm}^2$$

Standard Deviation = s = 1.4 cm

$$C.V. = \frac{s}{x} = 1.4 \frac{1}{17.5} = 0.08$$

$$S.E. = 0.32$$

Median = 17.6.

If the data are grouped into integer categories (Table 1, e.g., any value from 17.0 to 17.9 is assigned to integer category 17), then seven groups emerge.

Table 1. Length data grouped into integer categories.

Group	Number of Observations
14	1
15	2
16	4
17	6
18	4
19	2
20	1

These data can be plotted as a length-frequency histogram (Figure 15), and the mode of the distribution is 17 cm.

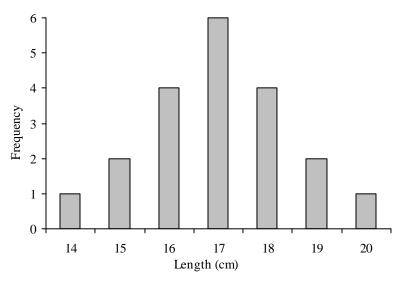


Figure 15. Length-frequency distribution.

Hypothesis Testing

Statistics are also used to compare data sets to evaluate hypotheses. The null or "no difference" hypothesis is considered with tests of significance. Two groups of data can be compared using the descriptive statistics for each group, or more appropriately using a *t*-test that pools the variance in the data sets. Groups of three or more can be evaluated using an Analysis of Variance (ANOVA).

The most rudimentary comparison between two groups of data compares the Confidence Intervals (*C.I.*) around the mean of each data set. If the *C.I.*s overlap, then we fail to reject the null hypothesis; that is, there is no detectable difference between the two groups at the stated significance level. If the *C.I.*s do not overlap, then there is a detectable difference at the stated significance level, and the null hypothesis is rejected.

The C.I. for a univariate data set is calculated using the mean, the standard error and a t statistic. The t statistic is used assuming the data are normally distributed and provides a factor to account for the probability of drawing the incorrect conclusion in the test. The t statistic is determined based on sample size and the specified significance level, but stabilizes at about 2 for large sample sizes and a confidence level of 95% (α =0.05). Tables of values for t statistics can be found in most introductory statistics books. C.I.s are calculated as follows:

$$C.I. = \overline{x} \pm \left(t_{(n-1)(\alpha/2)}\right) (S.E.)$$

where \overline{x} is the mean,

S.E. is the standard error, and

 $t_{(n-1)(\alpha/2)}$ is the t statistic for sample size n and significance level 1- α .

For the previous fork length data set, the *C.I.* is as follows:

$$17.5 \pm (2)(0.32) = 17.5 \pm 0.64 = 16.9 \le \overline{x} \le 18.1 \text{ cm}.$$

Example 4: Compare the fish length data from Example 3 to a similar data set collected at the same time from a different location. The null hypothesis is that there is no difference in the mean fish size between the two locations. If the mean fork length (\bar{x}) from the second pond is 16.4 cm and the *S.E.* is 0.30, then the *C.I.* is

$$16.4 \pm 0.60 = 15.8 \le \overline{x} \le 17.0$$
.

The C.I.s overlap and we therefore conclude that there is no detectable difference in mean fork length between the two data sets at the $\alpha = 0.05$ level. This can be shown graphically as a bar plot with C.I.s around the mean (Figure 16).

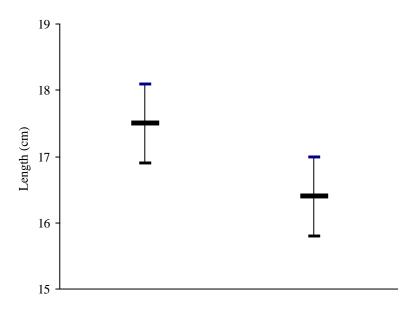


Figure 16. Mean and confidence intervals of fish fork lengths.

Fitting Models to Data

Considerable effort in fish stock assessment is devoted to fitting models to data to make predictions. The concept is referred to as regression analysis. The procedure fits a specified model (function) to a data set by estimating values for model parameters that minimize the sum of squared errors between observed and predicted values. The particular parameters that minimize the sum of the squared errors are considered the "best fit" for that model.

Linear regression analysis is the simplest form of model fitting. More complex functions are sometimes transformed to linear functions for analysis, or non-linear regression method are used to fit the model to the data

Example 5: Consider the estimation of a weight-length relationship for a given species of fish. The general model is as follows:

$$W = aL^b$$

where W = the weight in grams,

L =length in centimeters,

a = a unit conversion coefficient, and

b = the volumetric expansion coefficient.

The function is linearized by taking the natural logarithm of both sides of the equation

$$ln W = \ln(a) + b * \ln(L)$$

which is analogous to the linear model: y = a' + b'x.

Given the following length and weight data, estimate the parameters a and b for this fish species:

$W(\mathbf{gr})$	L (cm)	ln(W)	ln(L)
9710	100	9.18	4.61
6020	85	8.70	4.44
3610	72	8.19	4.28
2620	65	7.87	4.17
1150	50	7.05	3.91
680	42	6.52	3.74
360	35	5.89	3.56

Using linear regression on the log transformed data, the values of the linearized parameters are:

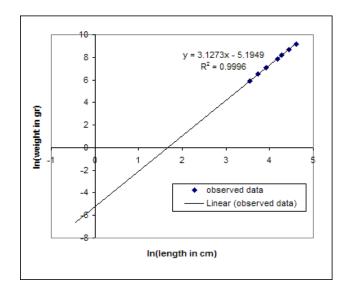
$$a' = -5.1949$$

 $b' = 3.1273$.

The value of a is the anti-ln (a'), and the value of b remains the same. Thus, the final value of the parameters in the model are:

$$W = 0.005545L^{3.1273}$$
.

The linear regression and non-linear regression are plotted in Figure 17.



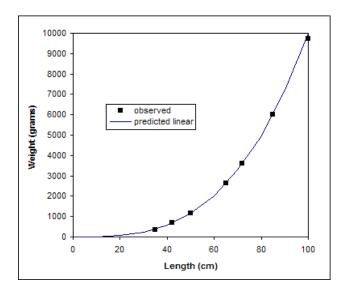


Figure 17. Linear (a) and non-linear (b) plots for the weight-length relationship: $W = 0.005545L^{3.1273}$, determined using linear regression methods.

An alternative method to fit this model to the data is using non-linear, least squares regression, where the sum of the squared differences between the observed and predicted weight values are minimized using Solver in EXCEL. The non-linear method begins with a table that includes the data, and two additional columns, one for predicted values of the dependent variable, and a another for the squared differences between the observed and predicted values. To

determine the predicted weight values, the model *a* and *b* parameters must first be guessed. Typically a good guess for a is 0.1, and for b is 3.

start a	start b
0.01	3
solver a	solver b
0.008324	3.034206

Obs L	Obs W	Pred W	(Obs-Pred)^2
100	9710	9744	1183
85	6020	5951	4746
72	3610	3596	184
65	2620	2637	286
50	1150	1190	1561
42	680	701	434
35	360	403	1854

10249

Solver in EXCEL is used to minimize the sum of the squared differences (residuals), while changing the parameters a and b. The results of the non-linear solution method are that a=0.0083 and b=3.0342.

Both methods can be used to fit the model to the data, and will result is similar results.

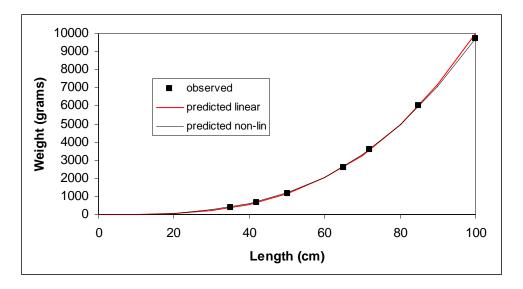


Figure 18. Plot showing the results of the linear and non-linear regression solutions for the weight-length relationship.

More complicated models can not be linearized, so in these cases non-linear regression is the only solution method available.

Exercises

1. Given the following data points (x, y values), plot the points, fit the linear model y = ax + b and obtain the best estimates of the parameters m and b. On the same graph, plot the predicted model.

2. Calculate the following.

$$10^3 10^{-1} 4^0 8^{\frac{2}{3}} 25^{-\frac{1}{2}}$$

3. Calculate the following.

$$Log_{10}(42.5)$$
 $ln(2.52)$

4. Determine the value of x.

$$0.70 = e^{-x}$$
 $10^4 = e^x$

5. Calculate $\frac{dy}{dx}$ for the following functions.

$$y = 3$$

$$y = e^{x}$$

$$y = 4 - 6x$$

$$y = 5x^{2} - 2x$$

6. Integrate the following.

$$\int_{1}^{2} x^{2} dx$$

$$\int_{0}^{2} e^{x} dx$$

$$\int_{0}^{4} (3+2x) dx$$

7. Compare the following length-frequency distribution using univariate descriptive statistics for each data set. Plot both L-F distributions as histograms on the same graph. Compare the means and the distributions around the means using confidence intervals.

Length (cm)	10	15	20	25	30	35	40	45	50
Group A	3	7	18	29	21	12	6	1	0
Group B	0	5	12	23	32	15	7	2	1

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Chapter III

GROWTH

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Introduction

The prediction of the length or weight of an aquatic animal as a function of age is a critical aspect of fish stock assessment. The growth of a fish, crustacean, or mollusc is rapid at a young age, slows at middle age, and stops at old age. The growth of an individual animal can be quite variable depending on food supply, environmental conditions, and genetic background. Therefore, the analysis of the age and growth of an aquatic animal requires large sample sizes.

Von Bertalanffy (1938) proposed a simple asymptotic function or model to describe the growth of fish by length, (*i.e.*, a curve for which the slope continuously decreases with increasing age, approaching an upper asymptote parallel to the *x*-axis) (Figure 1). Curves of weight at age also approach an upper asymptote, but form an asymmetrical sigmoid shape with an inflection occurring at a weight equal to about one third of the asymptotic weight (Figure 2).

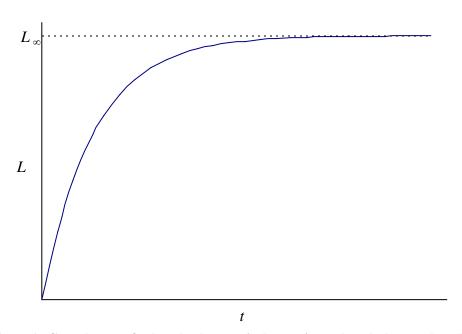


Figure 1. Growth curve for length where L_{∞} is the maximum length that can be achieved.

Input data for growth models may include length, weight, or age measurements. Length measurements may include total length, fork length, depth, girth, width, and height. Weight measurements may include total body weight, wet weight, dry weight, organ weight, shell weight, and meat weight. Age can be determined by counting growth rings that form in fish hard parts including scales, otoliths, and fin spines. Growth rings result from seasonal variation in

growth. Ages can also be inferred from multi-modal length-frequency distributions (e.g., for tropical fish species that exhibit little seasonal variation in growth and for some crustaceans) using graphical methods and computer based analysis (Figure 3).

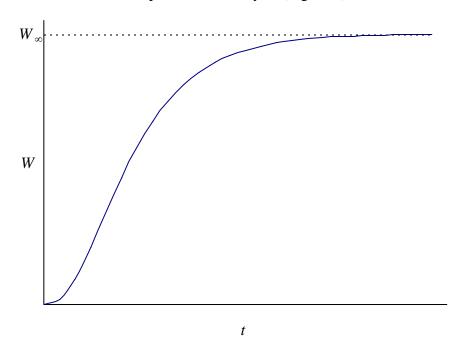


Figure 2. Growth curve for weight where W_{∞} is the maximum weight that can be achieved.

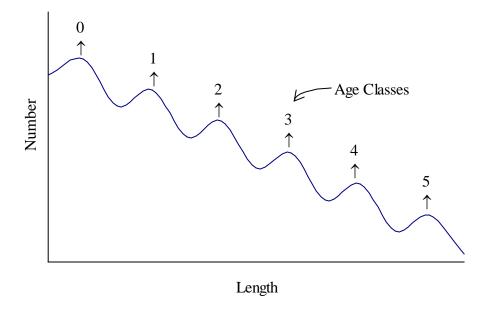


Figure 3. Multi-modal length-frequency distribution.

Von Bertalanffy Growth Equation

Estimating Length

The von Bertalanffy growth function states that the rate of growth $\frac{dL}{dt}$ is linearly related to length by the growth coefficient K (Figure 4):

$$\frac{dL}{dt} = K(L_{\infty} - L_{t}) = KL_{\infty} - KL_{t}$$

where L_{∞} is asymptotic length (*i.e.*, the value of L for which growth is zero), and t is age.

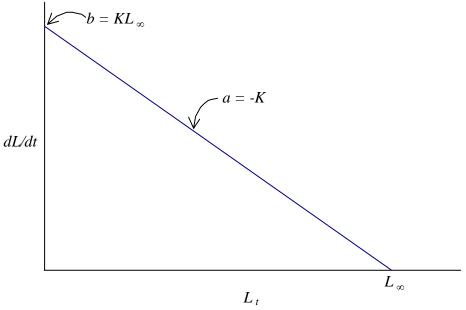


Figure 4. The linear relationship between growth rate (dL/dt) and length (L_t) .

Note that this function is in the form of the linear model:

$$y = ax + b$$

where
$$y \equiv \frac{dL}{dt}$$

 $x \equiv L_t$,
 $a \equiv -K$, and
 $b \equiv KL_0$.

The growth rate equation is a differential equation that is solved by the separation of variables technique. Rearranging and integrating yields:

$$\int \!\! \left[\int \!\!\! \left(L_{\infty} - L_{t} \right) \right] \!\! dL = \int K dt \; .$$

Based on integral tables,

$$-\ln[L_{\infty}-L_{t}]_{L_{0}}^{L_{t}}=Kt\int_{t_{0}}^{t}.$$

Assuming $t_0 = 0$ and $L_0 = 0$ and substituting,

$$-\ln\left[\frac{\left(L_{\infty}-L_{t}\right)}{L_{\infty}}\right]=Kt.$$

Taking the inverse natural log, or exponential, and rearranging yields:

$$\begin{aligned}
\left(L_{\infty} - L_{t}\right) / L_{\infty} &= e^{-Kt} \\
L_{\infty} - L_{t} &= L_{\infty} e^{-Kt} \\
- L_{t} &= \left(L_{\infty} e^{-Kt} - L_{\infty}\right) \\
L_{t} &= L_{\infty} \left(1 - e^{-Kt}\right).
\end{aligned}$$

Recall that a simplifying assumption was that at $t_0 = 0$, $L_t = 0$. In reality, most fish at age 0 have a finite length. Therefore, the equation is corrected by specifying t_0 , which is the age when length is equal to zero (Figure 5):

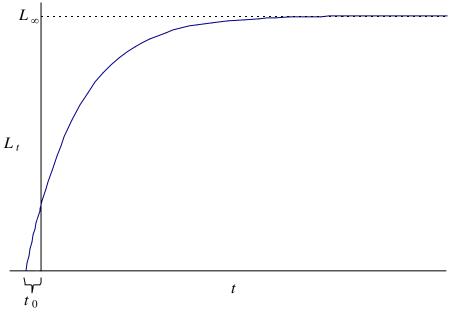


Figure 5. The corrected von Bertalanffy growth function for length $L_t = L_{\infty} \left(1 - e^{-K(t-t_0)} \right)$.

Using the mean of length at age data for young fish, t_0 is estimated by rearranging the von Bertalanffy function, solving for t_0 , and substituting values for t and L_t at the youngest age:

$$t_0 = t + \frac{1}{K} \ln \left(\frac{L_{\infty} - L_t}{L_{\infty}} \right).$$

The effect of the growth coefficient K on the growth curve for a given L_{∞} is shown in Figure 6. A value of K = 0.2 results in a gently ascending curve, whereas a value of K = 1.0 results in a rapidly rising curve.

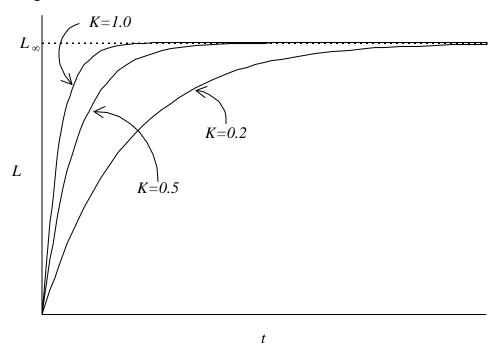


Figure 6. The effect of the value of the growth coefficient (K) on the growth curve.

Estimating Weight

The relation between the weight and length of an aquatic animal is expressed as:

$$W_t = aL_t^b$$

where a is a unit conversion coefficient

b is a volumetric expansion coefficient.

Von Bertalanffy assumed a value of b = 3 (*i.e.*, isometric or proportionally equal growth in length, breadth, and depth) and proposed the following:

$$W_{t} = W_{\infty} \left[1 - e^{-K(t-t_0)} \right]^3.$$

Estimating Age

The age of a fish at any length can be estimated by rearranging the von Bertalanffy equation:

$$t = \frac{1}{K} \ln \left(\frac{L_{\infty}}{L_{\infty} - L_{t}} \right) + t_{0}.$$

The span of age $(t_2 - t_1)$ between two lengths L_1 , L_2 is estimated as follows:

$$t_2 - t_1 = \frac{1}{K} \ln \left[\frac{\left(L_{\infty} - L_1 \right)}{\left(L_{\infty} - L_2 \right)} \right].$$

Estimating Growth Equation Parameters

Gulland-Holt Method

There are several classical methods for estimating von Bertalanffy growth model parameters using linear regression techniques. The Gulland-Holt method, based on the original rate equation, assumes uniform growth over an interval between two ages and plots that growth increment against mean length between the two ages (Gulland and Holt 1959).

That is:

$$\frac{dL}{dt} = K(L_{\infty} - L_{t})$$

or

$$\Delta L/\Delta_t = KL_{\infty} - KL_t$$

which has the form of the linear model:

$$y = b + ax$$

where K = slope

 $L_{\infty} = y$ -intercept/K.

Example 1: Given the following set of age and length data, where length represents the mean of a large number of fish measured at each age, estimate the von Bertalanffy growth model parameters using the Gulland-Holt method.

Age	Length (cm)	Growth Increment (cm)	Mean Length (cm)
(t)	$(L_{\rm t})$	$(L_{t+1}-L_t)$	$(L_{t+1}+L_t)/2$
1	25	11	30.5
2	36	6	39.0
3	42	5	44.5
4	47	4	49.0
5	51	2	52.0
6	53	1	53.5
7	54		

The data are fit by a linear model using a regression of the annual growth increment versus mean length (Figure 7). The value of K can be estimated from the negative of the slope (a); in this case a = -0.4, so K = 0.4. The y-intercept (b), gives an estimate of KL_{∞} which in this example equals 22.6 cm. Therefore,

$$L_{\infty} = \frac{b}{K} = \frac{22.6}{0.4} = 56.5 \text{ cm}.$$

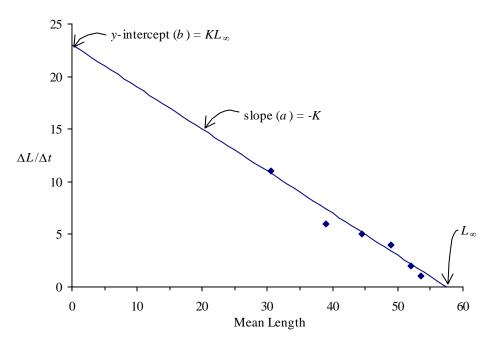


Figure 7. Gulland-Holt plot of growth rate against mean length.

The x-axis intercept (i.e., when $(\Delta L/\Delta t) = 0$), is a verification of the value of L_{∞} . The value of t_0 is estimated by taking the mean of t_0 obtained for the ages and lengths of the youngest fish when substituted into the rearranged von Bertalanffy function with the parameters K = 0.4 and $L_{\infty} = 56.5$ cm:

for
$$t = 1$$
 and $L_t = 25$,

$$t_0 = 1 + \frac{1}{0.4} \ln \left(\frac{56.5 - 25}{56.5} \right) = -0.46,$$

and for t = 2 and $L_t = 36$,

$$t_0 = 2 + \frac{1}{0.4} \ln \left(\frac{56.5 - 36}{56.5} \right) = -0.53.$$

The mean t_0 is -0.495.

In summary, the von Bertalanffy growth model parameters for this length and age data are:

$$K = 0.4$$

 $L_{\infty} = 56.5$ cm
 $t_0 = -0.495$.

Ford-Walford Plot

An alternative method to determine the parameters K and L_{∞} is the Ford-Walford plot (Walford 1946). This method requires equal time increments (T) between obtaining measures of fish length. The length of a fish at the later time (L_{t+T}) is plotted on the y-axis against the length of the fish at an earlier time (L_t) on the x-axis.

The derivation of the Ford-Walford plot is based on the von Bertalanffy function for ages t and t+T:

$$L_{t} = L_{\infty} (1 - e^{-Kt})$$
 and $L_{t+T} = L_{\infty} (1 - e^{-K(t+T)})$.

Subtract L_t from L_{t+T} and solve for L_{t+T} :

$$\begin{split} L_{t+T} - L_t = & L_{\infty} \Big[1 - e^{-K(t+T)} \Big] - L_{\infty} \Big[1 - e^{-Kt} \Big] \\ L_{t+T} - L_t = & L_{\infty} e^{-Kt} \Big[1 - e^{-KT} \Big] \\ L_{t+T} = & L_{\infty} e^{-Kt} \Big[1 - e^{-KT} \Big] + L_t \,. \end{split}$$

Substituting $L_{\infty}e^{-Kt} = -(L_t - L_{\infty})$ into the above equation and simplifying yields:

$$L_{t+T} = -(L_t - L_{\infty})(1 - e^{-KT}) + L_t$$

$$L_{t+T} = L_{\infty}(1 - e^{-KT}) + L_t e^{-KT}.$$

Note that this equation has the form of the linear model y = b + ax

where
$$y = L_{t+T}$$
,
$$x = L_t$$
,
$$a = e^{-KT}$$
, and
$$b = L_{\infty} (1 - e^{-KT})$$
.

The plot of L_t versus L_{t+T} forms a straight line regression that intersects the 45 ° line (Figure 8). The 45 ° line describes the function $L_{t+T} = L_t$, which indicates no growth between the earlier and later measurements. The intersection between the no growth function and the data regression line is L_{∞} .

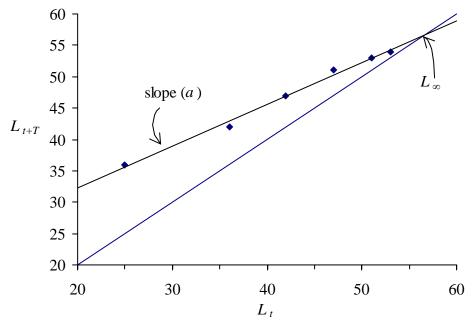


Figure 8. Ford-Walford plot of growth at time t+T versus length at time t.

The slope of the regression line is $a = e^{-KT}$. The value of K can be obtained by rearranging this equation to

$$K = -\left(\frac{\ln(a)}{T}\right).$$

If T = 1, this equation simplifies to $K = -\ln(a)$.

Example 2: Given the age-length data in Example 1, use the Ford-Walford plot method to estimate K and L_{∞} .

The data are fit by a linear model using a regression of the length of a fish at the later time versus length of the fish at an earlier time (Figure 8). To solve for L_{∞} , a 45° line (line of no growth) is added to the graph and then the no growth equation (y = x) and the regression line (y = 18.94 + 0.667x) are set equal to each other:

$$x = 18.94 + 0.667x$$

 $0.333x = 18.94$
 $x = 18.94/0.333$
 $x = 56.88$.

Therefore, the value of L_{∞} is 56.88.

The value of K is obtained using the equation:

$$K = -\ln(a)$$
.

The slope a is 0.667, therefore $K = -\ln(0.667) = 0.4$. The t_0 value is calculated in the same manner as before.

In summary, the von Bertalanffy growth model parameters for this length and age data are:

$$K = 0.4$$

 $L_{\infty} = 56.8 \text{ m}$
 $t_0 = -0.45.$

Non-linear Regression Methods

A more direct method of fitting the von Bertalanffy growth function to length or weight and age data is to use non-linear regression methods. Non-linear regression methods use a computer algorithm to iteratively fit new parameter values to the model until the sum of the squared differences between the observed and predicted values is minimized. The **Solver** routine in *Microsoft Excel* is a useful tool to conduct such an analysis on data entered in a spreadsheet.

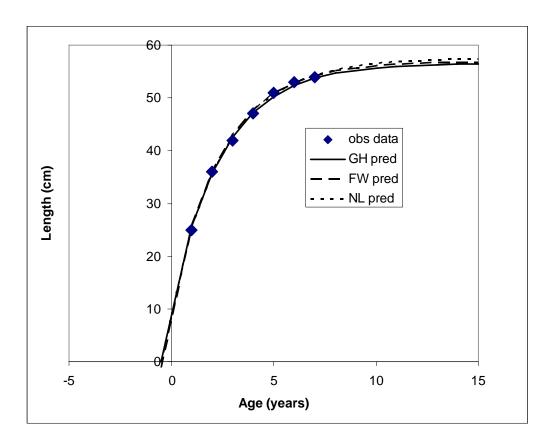
Example 3: The following spreadsheet was constructed in *Excel* given the previous length-age data set, and estimated values for K and L_{∞} of 0.4 and 57, respectively. Note that the values of L_{∞} and K are set aside as adjustable cells (cells C12 and C13), so that **Solver** can change the values as it attempts to minimize the sum of the squared differences (cell D9).

Column	A	В	C	D
Rows 1	AGE	$L_{ m obs}$	$L_{ m pre}$	$(L_{ m obs} ext{-}L_{ m pred})^2$
2	1	25	-	-
3	2	36	-	-
4	3	42	-	-
5	4	47	-	-
6	5	51	-	-
7	6	53	-	-
8	7	54	-	-
9				SUM(D2:D8)
10				
11				
12		K =	-	
13		$L_{\infty}=$	-	
14				
15				

Example 4: Compare the results of the three methods of fitting the von Bertalanffy model to data.

The results of the three methods used to estimate the parameters of the von Bertalanffy gowth model are compared in the following table and graph. The sum of the residuals squared was estimated for each of the sets of parameter estimates, and the smallest sum reflects the best model fit, that is the non-linear method. Note that this is only true if one is comparing the fits of various methods to the same model with the same number of parameters.

Parameter	G-H	F-W	N-L
K	0.40	0.41	0.39
Linf	56.51	56.88	57.48
to	-0.50	-0.45	-0.49
SSR	1.88	1.96	1.23



 $Figure \ 9. \ A \ comparison \ of \ the \ results \ of \ three \ methods \ used \ to \ fit \ the \ von \ Bertalanffy \ growth \ model \ to \ a \ single \ set \ of \ data$

Gompertz Growth Equation

Another growth curve that is sometimes used to describe the increase in fish weight with age is the Gompertz function (Ricker 1979):

$$W_{t} = W_{0}e^{\left[G\left(1-e^{gt}\right)\right]}$$

where W_t is weight at time t,

t is the age of fish,

 W_0 is a hypothetical weight at t = 0,

Gg is an instantaneous growth parameter when t = 0, and

g is the instantaneous rate of decrease of the instantaneous rate of growth.

The Gompertz function has a sigmoid shape with an upper asymptote of W_0e^G at $t=\infty$ and a lower asymptote of W=0 at $t=-\infty$. The inflexion point is W_{∞}/Q .

The Gompertz function is used primarily to describe data on weight at age, especially at young ages where growth is rapid. Note that there are three parameters to be estimated $(W_0, G, \text{ and } g)$, requiring non-linear estimation techniques for large data sets.

Exercises

1. Given the following mean lengths at age data set for mackerel, determine K, L_{∞} , and t_0 using Ford-Walford and non-linear methods.

Age	Length
1	15.1
2	22.7
3	27.5
4	32.3
5	34.8
6	37.1

2. Given the following mean lengths at age for herring, determine K, L_{∞} , and t_o using Gulland-Holt and non-linear methods.

Age	Length
3	25.7
4	28.4
5	30.2
6	31.7
7	32.8
8	33.7
9	34.4
10	34.9
11	35.6
12	36.0
13	35.9
14	37.0
15	37.7

3. Given the following subset of age-length data for striped bass, estimate K, L_{∞} , and to using non-linear methods on the individual observations. Note that there are multiple lengths at each age reflecting natural variation in growth. Compare the result to a non-linear estimation based on mean lengths at age for the same data. Note the differences in the values of the parameters estimated. What accounts for these differences, and which method is more appropriate?

Age	Lengths									
3	19									
4	18	19	21	21						
5	19	20	21	22	23	24	25	26		
6	18	19	21	22	24	25	26	28	29	
7	19	20	21	25	28	29	30			
8	23	24	26	28	28	29	30	31	32	34
9	22	30	31	32	33	34	35	36		
10	24	26	29	31	34	36	39			
11	26	29	33	34	35	36	36	38	39	
12	29	30	34	36	38					
13	41	42	43	44						
14	30	38								
15	34									
16	31									
17	47	52								
22	44									

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Chapter IV

ESTIMATION OF MORTALITY RATES

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Introduction

The general diagram of the dynamics of exploited fish stocks can be represented by an input-output diagram (Figure 1). Recruits into the stock and growth add to the total abundance and weight of the stock and are therefore considered inputs. Total losses from the stock are measured in two terms and are considered outputs. Natural mortality (M) is a measure of mortality resulting from natural causes (e.g., diseases, pollution, predation, aging), and fishing mortality (F) is a measure of mortality attributable to human harvest and discards.

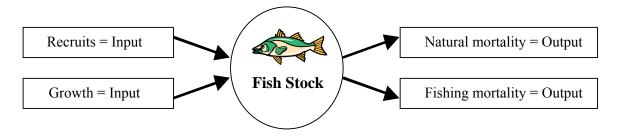


Figure 1. Schematic diagram of inputs and losses to a stock.

Mortality represents losses to a stock and is expressed as the rate of change of the size of a stock or a portion of the stock (e.g., cohort). It is generally most convenient to deal with instantaneous rates of change; *i.e.*, the rate at which the numbers in the population are decreasing. The term "instantaneous" infers that the number of fish that die in an "instant" is at all times proportional to the number present. The rate of loss can be expressed as:

$$\frac{dN}{dt} = -ZN$$

where Z = F + M is defined as the total instantaneous mortality coefficient. The differential equation has the form of a linear equation where the instantaneous total mortality rate (Z) is a constant of proportionality or the slope of the relationship between the rate of population loss(dN/dt) and the population size (N) (Figure 2).

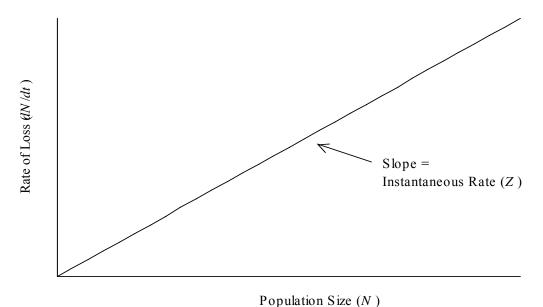


Figure 2. Relationship relationship between the rate of population loss $\left(dN\,/\,dt\right)$ and the population size $\left(N\right)$

Rearranging this equation:

$$-\left(\frac{dN}{ZN}\right) = dt$$

or

$$-\left(\frac{1}{ZN}\right)dN = dt .$$

Integrating the left side of this equation between N_0 and N_t yields:

$$\int_{N_0}^{N_t} \frac{1}{-ZN} dN = -\left(\frac{1}{Z}\right) \ln\left(\frac{N_t}{N_0}\right)$$

and integrating the right side between t_0 and t yields:

$$\int_{t_0}^t dt = t - t_0,$$

which is equal to t when $t_0 = 0$. Therefore,

$$\ln\left(\frac{N_t}{N_0}\right) = -Zt .$$

Rearranging and solving for N_t yields:

$$N_t = N_0 e^{-Zt}.$$

This solution is known as the exploited cohort equation, the population decay equation, or the survival equation because it describes the decline in numbers over time, and provides the number surviving at any time t. The parameter N_0 is the number of animals in the population at time 0 and N_t is the number at time t. The parameter Z is the total instantaneous mortality rate which can be separated into natural (M) and fishing (F) mortality (i.e., Z = F + M). Figure 3 shows the relationship between N_t and N_0 over time for various levels of mortality.

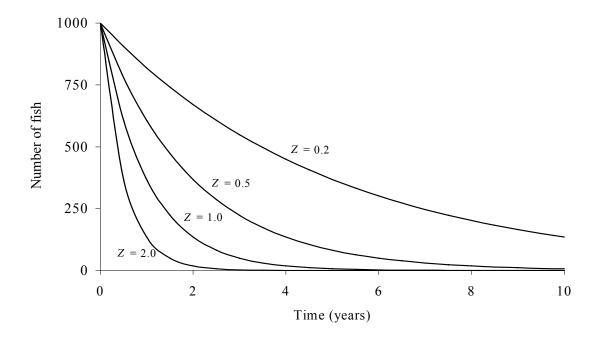


Figure 3. Exponential decay curves for Z = 0.2, 0.5, 1.0, and 2.0 with a recruitment N_0 of 1000 fish at age 0.

Example 1: If the instantaneous annual mortality rate is 2 (*i.e.* Z = 2) and the initial population size (N_0) is 1 million fish, how many will be alive at the end of the year.

If the year is apportioned into 12 months (*i.e.*, the "instant" time is one month), then 2/12 or 16.67% of the population will die each month. On the first month of the year, 166,667 fish will die $(1,000,000 \times 0.1667)$, leaving 833,333 alive. Similarly, 138,917 fish will die on the second month. If p is the proportion of fish that dies every day, then q = 1-p is the proportion of fish that survives. Table 1 describes the decrease in numbers over time.

At the end of the year, $[1,000,000 \times (1-0.1667)^{12}] = 112,156$ fish remain alive

If the year is apportioned into 365 days (*i.e.*, the "instant" time is one day), then 2/365 or 0.548% of the population will die each day. At the end of the year, $[1,000,000 \times (1-0.00548)^{365}] = 134,566$ fish remain alive

Table 1. Proportional decrease in population over time.

Time	Number of fish dead	Number surviving
1 st time interval	pN_0	qN_0
2 nd time interval	$p*q*N_0$	q^2N_0
3 rd time interval	$p*q^2*N_0$	q^3N_0
	•••••	
n^{th} time interval	$p*q^{n-1}*N_0$	$q^{n}N_{0}$

If a smaller 'instant' of time were used, for example an hour, 0.0228% of the population would have died by the end of the first time interval (an hour), leaving $[1,000,000 \times (1-0.000228)^{8760}]$ or 135,303 fish alive at the end of the year.

As the 'instant' of time becomes shorter and shorter, the exact answer to the number of animals surviving after 1 year is determined using the continuous form of the survival equation:

$$N_t = N_0 e^{-Zt} = 1,000,000 * e^{-2} = 135,335$$
 fish.

The proportion surviving at time *t* is equivalent to the number at the end of time *t* divided by the number at the start of time *t*:

$$S = \frac{N_t}{N_0} = e^{-Zt} .$$

Solving for *Z* gives:

$$Z = -\frac{\ln(S)}{t} .$$

If t is equal to 1, then:

$$Z = -\ln(S)$$

The total instantaneous rate of mortality equals the sum of the instantaneous rates of natural and fishing mortality (Z = F + M). Similarly, the total survival proportion (S_T), equals the product of the survival proportions from each source of mortality (*i.e.*, natural and fishing).

$$N_t = N_0 e^{-Zt} \Rightarrow N_t = N_0 e^{-(F+M)t}$$

and
$$S_T = S_F \times S_M .$$

If fishing mortality is equal to 0, then natural mortality is the sole cause of the cohort number decline. The natural mortality rate is directly related to the life span of the soecies (Table 2). Long-lived species, with life spans of 15 or more years have relatively low natural mortality rates ($M \le 0.2$). Short-lived species, with life spans of 5 years or less, have relatively high natural mortality rates ($M \ge 0.7$). Note that the life span of a species can be defined as the age of a cohort or years class when the population number is reduced to 5% of the strating number.

Table 2. Relationship between natural mortaity, percent annual loss, and life span

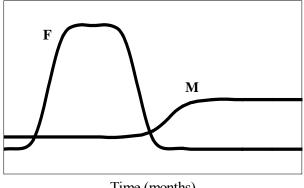
M instantaneous	Annual % loss	Life Span	
 0.05	5	60	
0.10	10	30	
0.20	18	15	
0.50	40	6	
0.70	50	5	
1.00	64	3	
1.50	78	2	

Example 2. Consider a species of fish with a five year life span (M=0.7). Develop a trajectory of cohort number as a function of age for a year class starting with 1000 individuals at age 0, considering natural mortality alone.

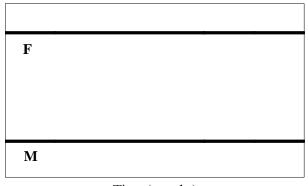
Solution: If M=0.7, then the proportion surviving, $S = e^{-M} = e^{-0.7} = 0.50$

Age (year)	Number	Annual % Loss	% Remaining
0	1000	50	100
1	500	50	50
2	250	50	25
3	125	50	12
4	62	50	6
5	31	50	3

The exact formulation used to calculate mortality rates depends on the relationship between natural and fishing mortality. A Type 1 fishery exists when natural mortality occurs at a time of the year other than the period of harvest (Figure 4). A Type 2 fishery exists when fishing and natural mortality occur simultaneously (Figure 5). Type 2 fisheries are more common.



Time (months)



Time (months)

For Type 2 fisheries, the natural and fishing mortality rates can be added together to determine total mortality rate, which can then be used in computations. For Type 1 fisheries, however, population size must be computed in two steps using the two mortality rates separately. Under the scenario shown in Figure 3, fishing mortality early in the year would reduce the population size upon which natural mortality would occur at the end of the year. To find the end of the year population size, apply fishing mortality to the initial population size to find a mid-year population size. The mid-year population size is then the starting population size upon which natural mortality is applied.

Annual mortality can also be measured in annual rates of exploitation, which can be defined as the annual percent removal rate (U). Exploitation rate can also be defined as the finite proportion of the population harvested (U = Catch/population size).

In a Type 1 fishery, where catch (C) occurs in the first half of the year (Figure 3), the exploitation rate U is calculated as

$$U = \frac{C}{N_0} = \left(1 - e^{-\frac{F}{2}}\right)$$

where F is the annualized fishing mortality rate.

In a Type 2 fishery, where fishing mortality and natural mortality occur simultaneously, the exploitation rate is calculated as

$$U = \frac{C}{N_0} = \left(\frac{F}{Z}\right)\left(1 - e^{-z}\right) = \left(\frac{F}{Z}\right)\left(1 - S\right)$$

Fishing mortality is generally not applied over the life span of a cohort, but is initiated when the fish recruit to the fishery based on age, size, or geographic reloaction. When fishing mortality is added to naturality mortality, the rate of decline of cohort number is accelerated (Figure 7).

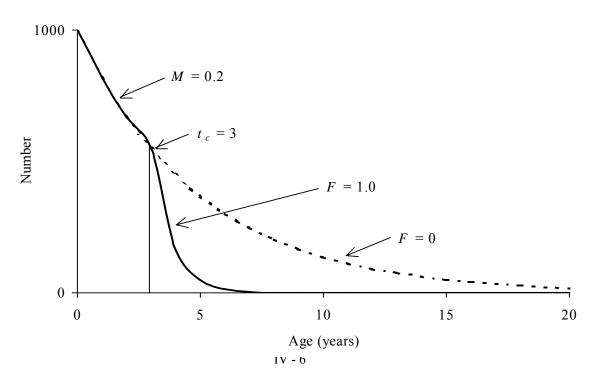


Figure 7. Exponential decay of cohort number when M=0.2, and F=1.0, applied at t_c, age 3.

Example 3: Consider a population of $N_0 = 1000$ fish at the start of the year. At the end of the year, $N_t = 358$ fish. During the year, 321 fish were caught. Calculate S, Z, U, F, and M during the year.

Solution:

$$S = \frac{N_t}{N_0} = \frac{358}{1000} = 0.358$$

$$Z = -\ln(S) = -\ln(0.358) = 1.027$$

$$U = \frac{C}{N0} = 321/1000 = 0.321$$

$$F = \frac{U * Z}{1 - e^{-Z}} = \frac{0.321 * 1.027}{1 - e^{-1.027}} = \frac{0.329}{0.64} = -0.514$$

$$M = Z - F = 1.027 - 0.514 = 0.513$$

Estimating Total Mortality from Catch Curve Analysis

Edser (1908) was the first to point out that when catches of North Sea Plaice were grouped into size-classes of equal breadth, the plot of the logarithms of the numbers of fish in each class had a steeply ascending limb, a dome shaped upper portion, and a long descending right limb, which was nearly straight through its entire length. This was soon recognized as a convenient method of representing catches graphically, and later became known as Catch Curve Analysis (CCA). This analysis is simply a graphical representation of the numbers of survivors plotted against age.

Recall the exponential decay function $N_t=N_0e^{-Zt}$ (Figure 3), when this function id linearized, the slope of the linear function is the total mortality Z (Figure 8).

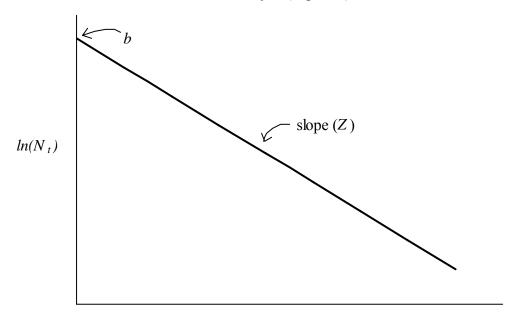


Figure 8. Plot of the linearized survuval equation adapted for catch curve analysis

In CCA, a linear regression of catch as a function of age is fit using the function

$$ln(Ct) = Zt + b$$

where t is time in years.

The absolute value of the slope, a, is equal to the total mortality Z. The variable b is the y-intercept. It is important that CCA be performed only on the portion of the stock that is fully recruited to the fishing gear. Also, the plus group is often not considered in catch curve analyses.

CCA is most appropriate for data from a single year class collected over time. If CCA is used for a single year's catch, it should only be done when there is no interannual trend in recruitment.

Example 4: Perform a catch curve analysis using the catch-at-age data for striped bass (*Morone saxatilis*) on the Atlantic coast from Maine to North Carolina (both landings and discards) reported by the Atlantic States Marine Fisheries Commission.

Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15+
Numbers	0.5	98	658	664	551	476	456	216	143	71	44	48	13	4.6	2.6
ln(N)	-0.69	4.59	6.48	6.49	6.31	6.16	6.12	5.37	4.90	4.26	3.77	3.86	2.58	1.52	0.95

Figure 9 shows the results of a catch curve analysis using this data. The CCA suggests that the average total mortality in 1996 on fully recruited cohorts is 0.51 (absolute value of -0.5104). The Atlantic States Marine Fisheries Commission assumed a natural mortality M between 0.15 and 0.2. Therefore, fishing mortality (F) was estimated to range between 0.31 and 0.36. The fisheries management target is set at F = 0.31.

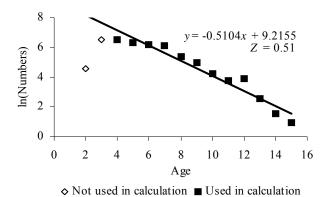


Figure 9. Catch curve analysis.

Catch curves are very simple to calculate, but they hide numerous assumptions that one has to consider when interpretting the results. Baranov (1914) described the assumptions involved in the interpretation of the catch curve analysis:

- 1. The survival rate is uniform with age, over the range of age-groups in question.
- 2. Since the survival rate is the complement of total mortality rate, and total mortality is composed of fishing and natural mortality, this will usually mean that each of these, individually, is uniform.
- 3. There has been no change in mortality rate with time.
- 4. The sample is taken randomly from the age-groups involved.
- 5. The age-groups in question were equal in numbers at the time each was being recruited to the fishery (constant recruitment).

If these conditions are satisfied, the right limb is a curve of survivorship which is both age-specific and time-specific. Two principal exceptions should always be kept in mind: 1) the decrease in vulnerability to fishing with age and 2) the consequent tendency toward an increase in survival rate will not be reflected in the catch curve and, in some instances, will introduce a bias in the estimates

The most common application of the catch curve is estimating mortality on a cohort from research survey data. If we collect a random sample using a trawl from a fish stock at a fixed time t, the mean catch at age per tow from one year to another can be used to estimate total mortality. The sample is characterized by its catchability which can be defined as the "catch capacity of the gear per one unit of effort". The relationship between CPUE or survey index (I) and the stock (N) can be written as:

$$I_{a,t} = qN_{a,t}$$

where $I_{a,t}$ is the survey index or mean catch per tow, q is the catchability coefficient, and $N_{a,t}$ is the cohort size at age a and time t.

The total mortality can be calculated from data for two or more consecutive years as follows:

$$Z = -\ln\left(\frac{N_{a+1,t+1}}{N_{a,t}}\right) .$$

Estimating Natural Mortality from Life History Characteristics

Natural mortality is difficult to measure directly. There is, however, a loose relationship between natural mortality and fish life history. In general, fish with early maturity, a high growth rate, and low longevity have high natural mortality. This includes pelagic fish such as anchovies, mackerel,

and herring. On the contrary, fish that mature late, have a slow growth rate, and live longer have low natural mortality. This includes demersal fish such as tautog, cod, sturgeon, and haddock.

Based on this and other generalizations about fish life history, several methods have been introduced that provide rough estimates of a species' natural mortality. The values for *M* obtained from these methods may not be accurate. Natural mortality is influenced by many factors other than life history. However, these methods can be used to get a handle on *relative* rates of natural mortality.

For example, Hoenig (1983) proposed the following formula that relates M to a species' longevity

$$M = \frac{2.98}{T_{\text{max}}} \approx \frac{3}{T_{\text{max}}}$$

based on the rearranged survival equation where N_0 is 1, N_t is 0.05 or 5% of the initial population number, and T_{max} is the maximum age or longevity of the species.

Pauly (1980) proposed a formula for tropical species that relates natural mortality with variables such as the growth parameter (K) and temperature (T). Gunderson (1980) relates natural morality to female gonadosomatic index.

Table 2 shows values of M for several species based on Hoenig's $3/T_{max}$ equation. It is important to remember that values derived from these methods represent only relative rates of natural mortality and may not be entirely accurate.

Table 3. Values of natural mortality derived using Hoenig (1983).

Species	Longevity (years)	<i>M</i> (Hoenig 1983)
	W /	`
Croaker	5	0.60
Menhaden	8	0.375
Bluefish	8	0.375
Cod	20	0.15
Striped bass	30	0.10
Tautog	30	0.10
Red Drum	50	0.06
Atlantic Sturgeon	60	0.05

Estimating Natural Mortality from Fishing Mortality and Effort Data

Paloheimo (1980) introduced a relationship between independent estimates of total mortality and fishing effort as follows:

$$F = qf$$

and

$$Z = F + M = qf + M$$

where f is fishing effort, and q is a catchability coefficient.

This is in the linear form of y = ax + b. Plotting Z against f and fitting the best line through the data, the resulting slope is an estimate of q and the intercept is an estimate of natural mortality M (Figure 10). These estimates, particularly M, should be treated with a little caution because the true fishing effort is not always accurately estimated by the available figures of nominal effort.

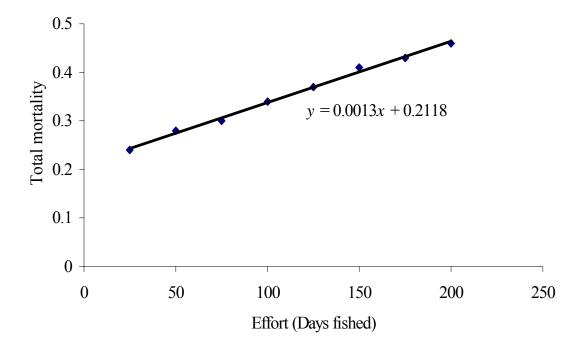


Figure 10. Plot of Z = qf + M. In this example, q = 0.0013 and M = 0.2118.

Example 6: Solve for *M* using the time series of effort and total mortality data in the kingfish fisheries off the coast of Thailand from 1966 to 1974.

Solution: Plotting the values of Z against f given in the table below results in Figure 11. The y-intercept estimate from the least squares regression equation gives an estimate of M = 2.05

Year	Effort (f) (x1000 days)	Z
1966	2.08	2.41
1967	2.08	2.69
1968	3.50	2.72
1969	3.60	2.62
1970	3.80	3.73
1971	-	-
1972	7.19	3.68
1973	9.94	4.61
1974	6.06	3.30

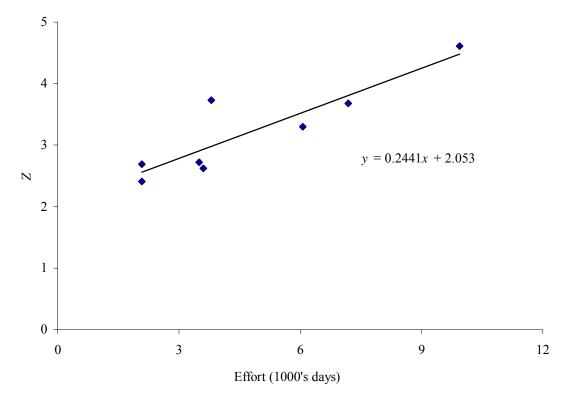


Figure 11. Linear regression of Z against f to solve for M.

Estimating Total and Fishing Mortality from Tagging Experiments

One method used to estimate parameters of a fish population is by tagging or marking a representative sample of the population, releasing them, and resampling at a later date to see what fraction of the population is tagged.

Tagging fish was first done to study movement and migration of individuals, but Petersen (1896) realized that tagging could also be used to measure population size and mortality rates. The

principal kinds of estimates that can be obtained from marking studies are:

- 1. Rate of exploitation
- 2. Size of the population
- 3. Survival rate of the population from one time interval to the next; most usefully, between times one year apart
- 4. Rate of recruitment to the population (Ricker 1975).

Not all mark and recapture experiments provide all this information. Estimating population size in a marine environment using mark-recapture techniques can be difficult, sometimes resulting in biased or imprecise estimates because of small capture and recapture probabilities. However, these problems are not encountered as often when estimating mortality rate.

One Time Releases or Single Census (Petersen Type)

Prior to a fishing season, C_1 fish are captured, marked and released; subsequently a sample of C_2 fish of which R were previously marked, is taken during the fishing season. Estimates of population size and exploitation rate of the population are given by:

$$\hat{N} = \frac{C_2}{U} = \frac{C_1 * C_2}{R}$$
 and $U = \frac{R}{C_1}$.

Variance for these estimates can be estimated with the following equations:

$$V\hat{a}r(\hat{N}) = \frac{C_1^2 C_2 (C_2 - R)}{R^3}$$
 and $V\hat{a}r(U) = \frac{R(C_2 - R)}{C_1^2 C_2}$.

The exploitation rate is converted to an instantaneous rate using either

$$II = 1 = e^{-F/2}$$

for a Type 1 fishery where the fishing mortality occurs in half the year, and natural mortality is small relative to fishing mortality, or

$$U = \frac{F}{Z}(1 - e^{-Z})$$

for a Type 2 fishery when natural and fishing mortality are occurring simultaneously. If natural mortality (M) is known (or assumed), estimates of fishing mortality can be found by substituting Z = F + M into either of these equations.

Example 6: The Northeast Utilities Service Company (NUSCO) in Waterford, CT has collected and tagged lobsters in Long Island Sound since 1978. Commercial fishers and others recaptured lobsters and returned the tags to the NUSCO. Recapture data for individual years of tagging were used to determine annual exploitation rates. The results of this study are shown in the following table. Given this information, calculate fishing mortality rate for each year, assuming

a natural mortality rate of M = 0.15.

Because fishing mortality and natural mortality occur at the same time, the instantaneous rate of mortality will be calculated using the Type 2 fishery equation:

$$U = \frac{F}{Z}(1 - e^{-Z})$$

$$U = \frac{R}{C_1} = \left(\frac{F}{F + M}\right)\left(1 - e^{-(F + M)}\right)$$

The left-hand side of the equation, exploitation rate (U) is known, but the equation can not be re-arranged to solve for F, as F is in both the denominator and numerator of the left hand side of the equation. The appropriate technique

to solve this equation is an iterative method, or in EXCEL Sover or Goal Seek can be used to estimate the value of F that makes the left hand side of the equation equal the right hand side of the equation. Setting M = 0.15, we can iteratively solve for F in *Microsoft Excel* using the **Goal Seek** or **Solver** procedures. For example in 1996, U = 0.16; thus F = 0.19 with an M = 0.15. In 1997, U = 0.27 therefore F = 0.34 and M = 0.15.

Year	Tagged	Recaptured	Rate of Exploitation
1986	5797	1194	0.21
1987	5680	1356	0.24
1988	6836	1727	0.25
1989	6436	1235	0.19
1990	5741	1066	0.19
1991	6136	1109	0.18
1992	9126	1842	0.20
1993	8177	1708	0.21
1994	7533	1974	0.26
1995	5307	963	0.18
1996	6221	997	0.16
1997	6102	1665	0.27

Recaptures in a Series of Years from a Single Year Release

In more complex tagging experiments, a known number of tagged fish are released at one time and recaptured over a period of several years. When more than two years of recaptures are available from a single release, *S* and *Z* can be estimated using a method similar to Catch Curve Analysis.

If N_0 fish are tagged initially, the number of tagged fish remaining in the population at the beginning of the r^{th} time interval is N_r , where

$$N_r = N_0 e^{[-(F+M)T]}$$

where *F* is fishing mortality rate, *M* is natural mortality rate,

 N_0 is the total number of fish tagged, and T is time.

The number of tagged fish captured in the r^{th} time interval (n_r) is given by:

$$n_r = \left[\frac{F}{(F+M)} \right] [N_r] \left[1 - e^{-(F+M)T} \right].$$

Substituting for N_r yields

$$n_r = \left[\frac{F_{(F+M)}}{F_{(F+M)}} \right] \left[N_0 \right] \left[e^{-(F+M)T} \right] \left[1 - e^{-(F+M)T} \right] .$$

Taking the natural log of both sides and substituting Z for (F+M) gives:

$$\ln(n_r) = -ZT + \left[\ln\left(\frac{FN_0}{Z}\right) + \ln\left(1 - e^{-ZT}\right) \right].$$

This equation can be rewritten in linear form as

$$\ln(n_r) = aT + b$$

where a is the negative of total mortality (-Z) (since a will be negative) T is time in years.

The natural log of recaptures plotted against time provides a negatively sloped linear function, similar to CCA.

Example 7: A sample of 1000 winter flounder were tagged in Narragansett Bay in the winter of 1990. Returns from those tagged fish from 1991 to 1994 are shown below. Determine estimates of total mortlaity (Z) and fishing mortality (F) over the time period, assuming a natural mortality rate of M = 0.30.

Year	n_r	$ln(n_r)$
1991	270	5.6
1992	36	3.6
1993	6	1.8
1994	1	0

Conducting a linear regression of $ln(n_r)$ as a function of time in years (Figure 12) provides an estimate of total mortality of Z = 1.8. If M = 0.3, then F = 1.5, an extremely high rate of fishing mortality.

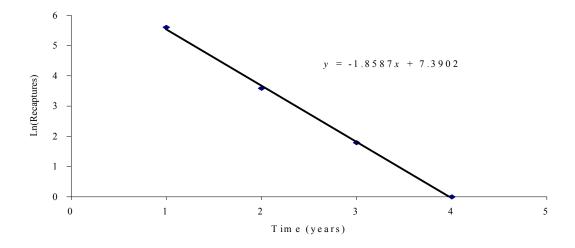


Figure 12. Ln(recaptures) versus time for tagged winter flounder.

These types of estimates hold assumptions of equal survivorship, complete reporting, and no tag loss or tag mortality. In the real world, these assumption are rarely satisfied and should be investigated by conducting parallel studies such as a tag reward program and special laboratory work on tag retention and tag induced mortality. Non-random mixing of tagged and untagged fish and emigration can also introduce bias and should be investigated.

Exercises

- 1. Given an initial population of $N_0 = 25,000$ fish, a survival rate of S = 0.47, and a commercial harvest of 10,500 fish, determine N_t , U, Z, F and M during the first year for both a Type 1 and Type 2 fishery. For the Type 1 fishery, assume fishing occurs only in the second half of the year.
- Weakfish caught by the NEFSC autumn bottom trawl survey were aged by applying annual age-length keys from pooled commercial and research samples to survey caught fish. Catch-at-age (expressed as CPUE) for the 1985 and 1990 year classes is shown below. Estimate total and fishing mortality for the two different years, assuming M = 0.25.

	Number at age								
Year	0	1	2	3	4	5			
1985	10.39	4.12	0.93	0.06	0.03	_			
1990	3.45	0.73	0.13	0.06	0.019	0.013			

Weakfish CPUE-at-age from NEFSC autumn bottom trawl survey.

3. The following data are taken from the Cooperative Striped Bass Tagging Program, conducted by the U.S. Fish and Wildlife Service and the Atlantic States Marine Fisheries Commission. The purpose of the program is to monitor mortality and migration of striped bass for the major producer areas (Hudson River, Chesapeake Bay, and Delaware Bay). This program comprises 4 critical operations: tagging fish, recovering tags, managing records of releases and recoveries, and analyzing recovery data. Total releases of tagged striped bass have exceeded 170,000 fish in ten years, through the participation of 10 states. Analysis of these data is performed on an annual basis by the Atlantic States Marine Fisheries Commission tagging group. Data from the Hudson River portion of this program are shown in the following table. Using this data, derive estimates of total and fishing mortality for the years 1990, 1993, and 1996. Natural mortality for striped bass is *M* = 0.15.

Release and recapture matrix of striped bass in the Hudson River from 1988 and 1996.

Year of	Number	Recaptures								
release	released	1988	1989	1990	1991	1992	1993	1994	1995	1996
1988	227	25	31	18	11	10	5	4	1	4
1989	387	23	41	29	17	9	6	8	4	0
1990	446			62	31	27	14	9	4	1
1991	364				38	31	12	10	9	4
1992	699					90	58	35	21	13
1993	537						73	36	24	18
1994	381							43	33	26
1995	462								50	34
1996	683									88

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Chapter V

SELECTIVITY OF MARINE FISH HARVESTING GEARS: RECRUITMENT TO THE FISHING GEAR AND THE FISHERY

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Background

Since the 1970's, considerable progress has been made in defining the selection characteristics of various fish harvesting gears. Fishery managers and fishing gear technologists have investigated the subtle characteristics of species-specific size selection as a function of mesh size and shape in trawls, mesh size and hanging ratio in gill nets, hook size and style in longlines, and mesh size and funnel opening size in traps, so as to provide improved management of fishery stocks harvested with these gear types.

Literature Review

The study of size selection characteristics of fish harvesting gear began in the early 1900's, with an application toward fishery management (Baranov, 1918 *in* Baranov, 1976). In the late 1950's, the International Commission for the Northwest Atlantic Fisheries (ICNAF) co-sponsored a special scientific meeting on the selectivity of fishing gear (Anonymous, 1963), and research summarized in the proceedings of that meeting were the basis for three decades of progress. The size selectivity of all fish harvesting gear can be classified broadly into two types of probability distributions (Clark, 1960, Holt, 1963; Pope et al., 1975):

- 1. A sigmoid curve, increasing from some positive value less than one to one as a function of fish size. This curve is represented by a logistic cumulative distribution function (LCDF). The selection characteristics of this curve are that all fish smaller than a particular size (L_1) are not captured (P=0); that all fish larger than a particular size (L_2) are captured (P=1); and that fish of a certain size (L_{50}) between L_1 and L_2 have a 50 percent probability of capture (P=0.5) if encountering the gear.
- 2. A dome-shaped curve, increasing from some positive value less than one to one, then decreasing again as a function of fish size. This curve is represented by a truncated, rescaled normal probability density function (NPDF). The characteristics of this curve are that all fish smaller than a particular size (L_I) and larger than another particular size (L_2) are not captured, and that fish of a certain size (L_{opt}) between L_I and L_2 have a 100 percent probability (P = 1.0) of capture if encountering the gear.

Fish size selection by a trawl codend may be modeled by a LCDF. Early work by Clark (1963) estimated sigmoid selection curves for groundfish species in the Northwest Atlantic. In the 1970s and 1980s additional research provided species- and mesh size-specific selection curves

(Smolowitz, 1983). More recent work has attempted to further define codend selectivity as a function of mesh shapes, (square versus diamond) and to relate mesh shape to codend escape survival (DeAlteris & Reifsteck, 1993). For fish selection by trawl codends, the following generalizations may be made: (1) larger meshes retain fewer small fish, shifting the selection curve to the right; (2) square mesh codends steepen the selection curve and shift it slightly to the right, as compared to a codend of similar mesh size of diamond shape.

Fish size selection by a gillnet may sometimes be modeled by NPDF (Hamley, 1975). Early work by Regier and Robson (1966) established an experimental methodology to describe the parameters of a normal distribution used to characterize the selectivity of the gillnet. Later work by Borgstrom (1989), and Hamley and Regier (1973) further defined the application of the NPDF distribution function to gillnet selection. More recently, Lazar and DeAlteris (1993), presenting the results of an analysis of gillnet selection in the Gulf of Maine groundfish fishery, used a truncated two-term gram Charlier series model to define in greater detail the shape of the selection curve.

Fish size selection by a longline with hooks may also be modeled by a sigmoid curve (McCracken, 1963 and Saetersdal, 1963). Ralston (1982), investigating the Hawaiian deep-sea handline fishery, concluded that a sigmoid curve most accurately described the selective properties of the gear in that fishery. Similar results were reported by Bertrand (1988) in his analysis of hook selectivity in the handline fishery of the Saya de Malha Banks (Indian Ocean). In contrast, Ralston (1990), investigating the size selection of snappers by hook and line gear, concluded that neither distribution model in its simplest form depicted hook selectivity. Otway and Craig (1993), studying the effects of hook size in catches of undersize snapper, also determined that neither the normal nor the logistic model was appropriate.

Fish size selection by traps has also been investigated. Stevenson and Stuart-Sharkey (1980) tested the effect of three different mesh sizes and found that increasing the mesh size led to a significant reduction in the number of smaller fish caught. Ward (1988), reporting on the results of mesh size experiments in the Bermuda trap fisheries, developed sigmoid-shape selection curves for the dominant species. However, as noted by Ward, since the traps had very large funnel openings relative to the maximum fish size in the population, nothing prevented entry by even the largest fish. Bohnsack et al. (1989) investigated the effect of fish trap mesh size on reef fish off southeastern Florida and found that larger meshes retained fewer small fish. It is clear that the mesh covering a trap will affect the retention of the smaller fish. If there is no restriction to entry by the largest fish in the population, then the selection curve may be sigmoid. However, the traps with the highest catch efficiency will have funnel openings small enough so as to impede the exit of captured fish that would otherwise be retained by the mesh size. Therefore these traps may have a dome-shaped selection curve.

General Theory

Logistic Cumulative Distribution Function

The size selection characteristics of trawl cod-end meshes and some hooks can be represented by a logistic cumulative distribution function (LCDF) (Figure 1) of the form

$$PL_L = (1 + e^{(-\alpha 2*(L-L_{50}))})^{-1}$$
.

where PL_L is the probability of retention at length (L) $\alpha 2$ is the steepness of the curve, and L_{50} is the length at 50% selection.

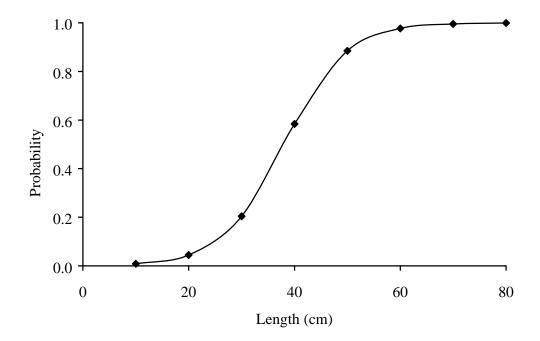


Figure 1. Probability of selection following a logistic cumulative distribution function.

This equation is a specialized form of the general LCDF equation:

$$PL_L = \left(1 + e^{\left(-(\alpha + \beta L)\right)}\right)^{-1}$$

where: α is $(-\alpha 2 * L_{50})$, or $(-\beta * L_{50})$

 β is identical to $\alpha 2$, the steepness of the curve.

The terms α and β can be determined using:

- 1. Non-linear regression of data relating PL_L and L, or
- 2. Linear regression (Figure 2) of the linearized LCDF using the equation:

$$ln(P/(1-P)) = \alpha + (\beta * L)$$

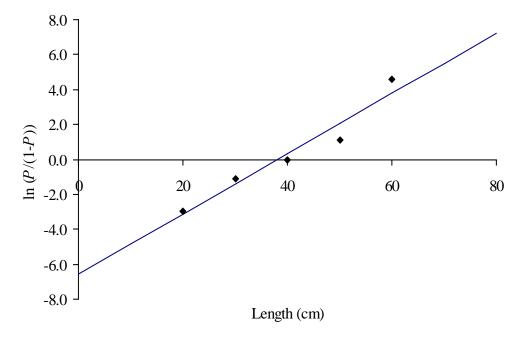


Figure 2. Regression of ln(P/(1-P)) vs L.

The LCDF curve is unique for a particular fish species, mesh size and mesh shape. The selection factor (*SF*) is defined as:

$$SF = L_{50}/ml$$

where *ml* is the stretched mesh length.

The selection range (SR) is a measure of the steepness of the LCDF curve, and is described by:

$$SR = L_{75} - L_{25}$$

where L_{75} is the length at P = 0.75, and L_{25} is the length at P = 0.25.

Using the selection factor, the L_{50} of other mesh sizes can be determined, resulting in a family of selection curves for a given species and mesh shape (Figure 3).

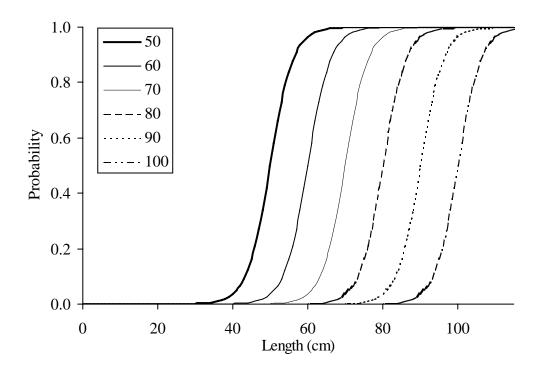


Figure 3. Logistic cumulative distribution function (LCDF) selectivity curves

Normal Probability Distribution Function

The size selection characteristics of gillnets and some traps are represented by a truncated, scaled normal probability distribution function (NPDF) (Figure 4):

$$PN_L = e^{\left[-\left(L-L_{opt}\right)^2/\left(2*SD^2\right)\right]}$$

where PN_L is the probability of capture at length (L)

SD is the standard deviation, and

 L_{opt} is the length of maximum selection probability.

The parameters L_{opt} and SD which define the NPDF can be determined by comparing the catches of two similar gears (A and B) that overlap in length-frequency distributions (Holt, 1963). The method regresses the natural log ratio of the catches of the two gears at given lengths against lengths (Figure 5) using the linear model:

$$y = a + bL$$

where y is the $ln(C_B/C_A)$, a is the y-intercept, and b is the slope.

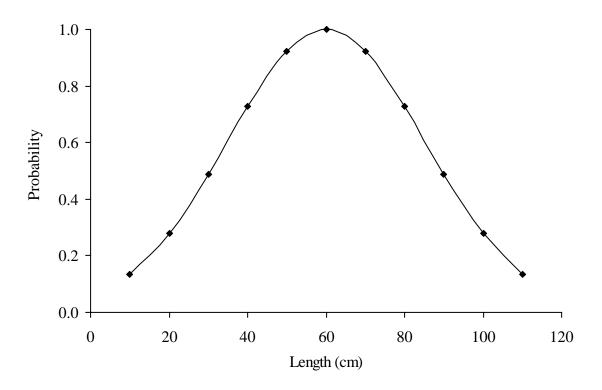


Figure 4. Probability of selection following a normal probability distribution function.

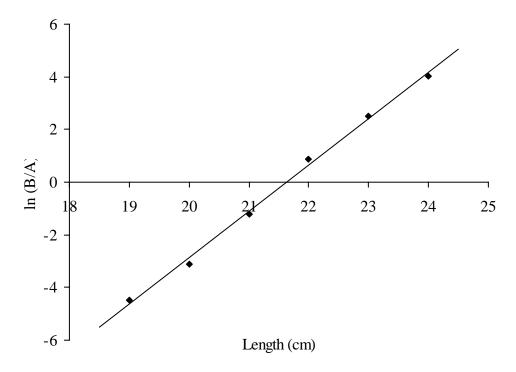


Figure 5. Linear regression of $ln(C_B/C_A)$ for two similar gears that follow NPDF.

 L_{opt} and SD for the two gears can be determined with the following equations using the parameters a and b, and the mesh sizes of the two gears ml_A , and ml_B :

$$L_{opt}A = -2*[(\alpha*ml_A)/(b*(ml_A + ml_B))]$$

$$L_{opt}B = -2*[(\alpha*ml_B)/b*(ml_A + ml_B))]$$

$$SD = [-2*\alpha*(ml_B - ml_A))/(b^2*(ml_A + ml_B))]^{1/2}$$

The selection factor SF is:

$$SF = L_{opt}/ml$$

where ml is the mesh size.

Using the selection factor, the L_{opt} , of other mesh sizes can be determined, resulting in a family of selection curves for a given species (Figure 6).

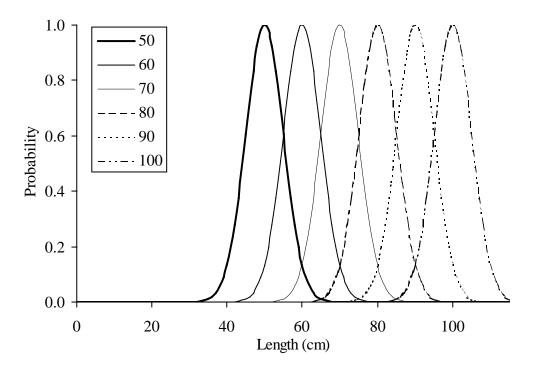


Figure 6. Normal probability distribution function (NPDF) selectivity curves.

Field Experiments and Estimation of Size Selection Curves

The selection characteristics of fish harvesting gears are usually determined using comparative fishing trials.

For LCDF selection, the probability of capture or retention approaches 100% (P=1) for the largest fish in the population, and the smallest fish in the population have a probability of capture or retention approaching 0% (P=0). Therefore, the comparative fishing experiment compares the catch of a relatively larger hook or mesh to the catch of a small hook or mesh that captures or retains all the fish that would encounter the larger gear, but be only partially captured or retained.

In the case of a trawl cod-end mesh experiment, the comparative trials are conducted using:

- 1. a covered cod-end, where the catch retained in the cod-end is compared to the catch of the cover and the cod-end.
- 2. a trouser trawl with two cod-ends, small mesh and experimental, where the catch retained in the experimental cod-end is compared to the catch retained in the small mesh cod-end.
- 3. alternate paired tows aboard a single or paired vessels where the catches of the small mesh cod-ends are compared to the catches of the large mesh cod-ends.

Example 1: Covered cod-end experiment for an idealized roundfish.

The catches by length (cm) for a mesh cover and an experimental cod-end (12 cm, diamond mesh) are shown in Table 1. Solve for L_{50} , selection factor, selection range, and the parameters α and β that define the LCDF.

L (cm)	Cover	Cod-end	Sum	Ratio (P)
10	10	0	10	0.00
20	19	1	20	0.05
30	75	25	100	0.25
40	200	200	400	0.50
50	100	300	400	0.75
60	2	198	200	0.99
70	0	50	50	1.00
80	0	5	5	1.00

Table 1. Catch data from covered cod-end experiment.

The selection curve is plotted, and graphically the L_{50} is estimated to be 40 cm, in addition the L_{75} and L_{25} are estimated to be 50 and 30 cm, respectively. The selection factor is 40 cm/12 cm = 3.3, and the selection range is L_{75} - L_{25} = 20 cm

The parameters, α and β , defining the generalized LCDF equation are determined indirectly using linear regression on the transformed equation. These results are illustrated in Table 2 and Figure 7. Alternatively, the parameters, $\alpha 2$ and L_{50} , can be estimated directly using non-linear least squares regression on the specialized form of the LCDF equation .

L (m)	Cover	Codend	Sum	Ratio (P)	ln (P/1-P)	Predicted P
10	10	0	10	0.00		0.008
20	19	1	20	0.05	-2.94	0.042
30	75	25	100	0.25	-1.10	0.198
40	200	200	400	0.50	0.00	0.582
50	100	300	400	0.75	1.10	0.887
60	2	198	200	0.99	4.60	0.978
70	0	50	50	1.00		0.996
80	0	5	5	1.00		0.999

Table 2. Results of the covered cod-end experiment.

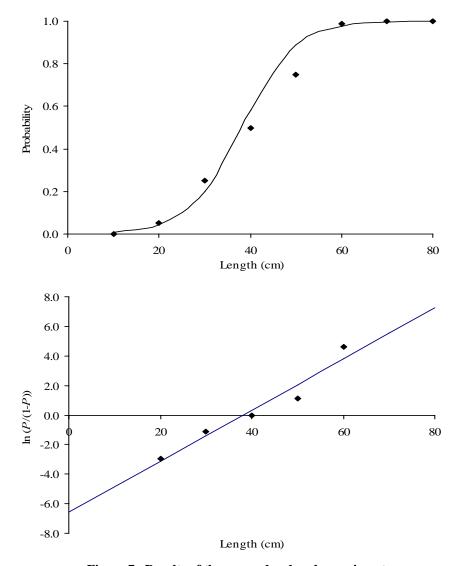


Figure 7. Results of the covered cod-end experiment.

For NPDF selection, the probability of retention or capture approaches 100% (P=1) for a particular size of fish, then decreases to 0% (P=0) for smaller and larger fish. Therefore, a comparative fishing experiment compares the catch of a particular size mesh in a gillnet or combination of wall mesh and entrance funnel in a trap to similar gears smaller or larger. The length-frequency distributions for the catches of the two gears must overlap for comparison to be effective. In the case of the gillnet, a dome-shaped selection curve reflects capture by wedging or gilling. The catch comparison assumes that the two nets with different mesh sizes have similar fishing power and standard deviations for the selection curves.

Example 2: Gillnet catch comparison experiment for two nets.

Nets A and B have mesh sizes of 8.1 and 9.1 cm respectively. Catches from these two nets are shown in Table 3. Determine the selection parameters a and b, the $L_{opt}s$ for both nets, the standard deviation, and selection factor. Plot the results using the NPDF model.

Length	# Captured A	# Captured B	ln(B/A)
18	20	0	-
19	90	1	-4.5
20	199	9	-3.1
21	182	53	-1.2
22	119	290	-0.9
23	29	357	2.5
24	4	225	4.0
25	0	101	_

Table 3. Data from a fishing experiment comparing two similar gill nets.

Plotting the length-frequency distributions for the catches of the two nets, the required overlap is observed (Figure 8a).

Regressing the $\ln(B/A)$ against L (Figure 8b) and fitting the model: y = bx + a, results in coefficients:

$$a = -38.1$$

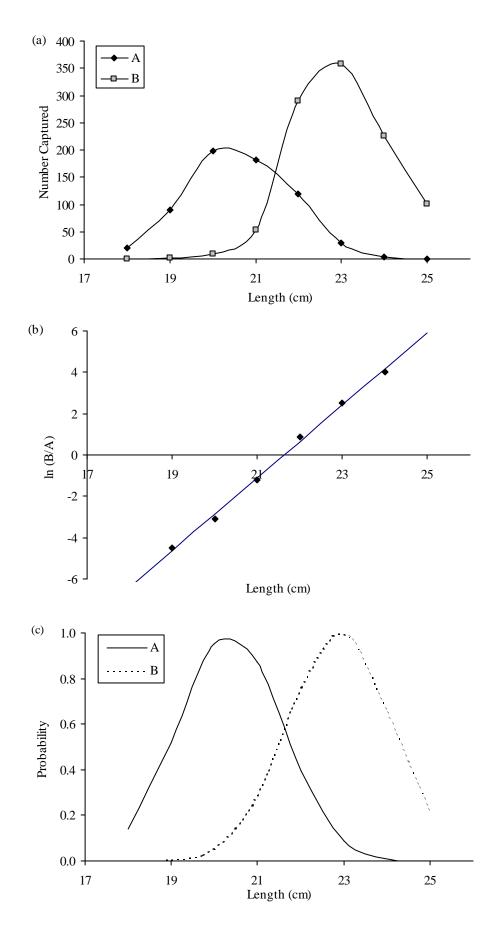
 $b = 1.76$

Following the method of Holt (1963):

$$L_{opt} A = 20.4 \text{ cm}$$

 $L_{opt} B = 23.0 \text{ cm}$
 $SD = 1.44$
 $SF = 2.5$

Applying these values to the parameters of the NPDF model results in the selection curves shown in Figure 8c.



 $\label{eq:Figure 8. Analysis and results of NPDF selectivity analysis. }$

Exercises

TRAWL COD-END SELECTION PROBLEM COVERED COD-END EXPERIMENT

Yellowtail flounder on Georges Bank

Cod-end = 14 cm, diamond mesh; Cover = 5 cm, square mesh

Fish Length (cm)	Cod-end	Cover
10-12	0	0
13-15	0	50
16-18	10	102
19-21	20	90
22-24	33	60
25-27	48	43
28-30	107	21
31-33	95	5
34-36	87	0
37-39	60	0
40-42	60	0
43-45	20	0
46-48	12	0
49-51	2	0
52-54	0	

- 1. Determine the selection curve by linear regression on natural log transformed data
- 2. Based on the selection curve, estimate the L_{50} , SF, SR for yellowtail flounder, using a 14 cm diamond mesh cod-end.

TRAWL COD-END SELECTION PROBLEM <u>ALTERNATE TOW EXPERIMENT</u>

Cod on Georges Bank

Exp Trawl = 14 cm, diamond mesh; Lined Trawl= 5 cm

Fish Length (cm)	Lined Trawl	Exp Trawl
11-15	0	0
16-20	5	0
21-25	7	0
26-30	2	0
31-35	10	0
36-40	30	2
41-45	36	6
46-50	42	8
51-55	50	20
56-60	83	35
61-65	64	42
66-70	53	47
71-75	42	38
76-80	19	20
81-85	11	10
86-90	7	7
91-95	6	5
96-100	4	3
101-105	1	1
106-110	0	0

- 1. Determine the selection curve by non-linear regression of PL_L versus L.
- 2. Based on the selection curve, estimate the L_{50} , SF, SR for cod using a 14 cm diamond mesh cod-end.

GILLNET SELECTION PROBLEM FOR COD

Fish Length (cm)	Webbing 13.6 cm	Webbing 14.8 cm	Webbing 16.0 cm
46	0	0	0
48	5	0	0
50	26	0	0
52	52	1	0
54	102	16	4
56	295	131	17
58	309	362	95
60	118	326	199
62	79	191	202
64	27	111	133
66	14	44	52
68	8	14	25
70	7	8	15
72	0	1	5
74	0	0	1
76	0	0	0

- 1. Determine parameters a and b for each paired comparison.
- 2. Determine *SD* for each paired comparison.
- 3. Determine L_{opt} for 13.6, 14.8, 16.0 cm webbing.
- 4. Average the parameters a, b, and SD resulting from the two paired comparisons.
- 5. Plot L-F and selectivity curve for each webbing.

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Chapter V1

YIELD PER RECRUIT (YPR) AND SPAWNING STOCK BIOMASS PER RECRUIT (SSBPR) MODELS

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Background

Yield per recruit (YPR) models are useful to fishery resource managers for predicting the effects of alterations in harvesting activity on the yield available from a given year-class or cohort (Gulland 1983). Two elements that define the model and that are usually regulated by resource managers are fishing mortality (*F*) and the pattern of harvesting activity on different sizes of fish. Often the latter element has been simplified by assuming knife-edge selection (100% vulnerability at age of first capture), so that Beverton and Holt's (1957) analytical solution to the yield equation could be applied (Gulland 1969, 1983; Pauly 1984; Ricker 1975; Saila et al. 1988; Sparre et al. 1989). While this assumption may be appropriate for size selection that follows a logistic distribution function, as is sometimes observed in a trawl codend, the Beverton-Holt yield equation does not incorporate recent advances in understanding the size selection processes of the principal gear types used on groundfish (trawls, traps, gillnets, and longlines).

The purpose of this chapter is to review the analytical solution to the YPR model assuming knife-edge selection, and to describe the integration gear-specific size selection into YPR and spawning stock biomass per recruit (SSBPR) discrete time models. The development of a generalized model applied to a hypothetical or "idealized" roundfish is used as a prelude to the application of the model to specific marine fish species using actual selectivity data for harvesting gear, either presently used in the fisheries or proposed for future use.

Analytical Solution

To predict the yield from a given number of recruits in a single cohort of fish, parameters characterizing the life history of the fish species and affecting the harvest of the stock must be specified. While the life history parameters affect the potential biomass available from the cohort, harvest related factors are controlled by fisheries management to ultimately affect the yield taken from the biomass. The biological or life history parameters affecting the potential maximum biomass and the timing of the maximization are:

K is the instantaneous growth coefficient, M is the instantaneous natural mortality coefficient, and W_{∞} is the maximum weight an individual fish may attain.

The fishery related factors affecting the maximum potential yield are:

 t_c is the age at which the fish enter the fishery (controlled by mesh size in a trawl fishery), and

F is the instantaneous fishing mortality coefficient.

If *R* recruits from a cohort at time t = 0, then the numbers of fish caught (dC_t) and the yield in weight (dY_t) from that catch can be defined in short time intervals (t, t + dt) by:

$$dC_t = F_t * N_t * dt$$

and

$$dY_t = F_t * N_t * W_t dt$$

where N_t is the number of fish alive at age t,

 F_t is the fishing mortality coefficient, which may vary with age, and

 W_t is the average weight of an individual fish at age t.

The total catch in numbers (C) from a cohort or yield in weight (Y) results from the integration of the previous differential equations from the age at which the fish remaining in the cohort enter the fishery (t_c) to some limiting age t_L .

$$C = \int_{t_c}^{t_L} dC_t = \int_{t_c}^{t_L} F_t N_t dt$$

$$Y = \int_{t_c}^{t_L} dY_t = \int_{t_c}^{t_L} F_t N_t W_t dt$$

Making the following assumptions simplifies the problem:

$$\begin{split} F_t &= 0 \text{ and } t < t_c \\ F_t &= F = \text{constant for } t \ge t_c \\ Z_t &= M \text{ for } t < t_c \\ Z_t &= F + M \text{ for } t \ge t_c \\ N_t &= R \ e \Big[- M^{(t - t_c)} \Big] \text{ for } t < t_c \end{split}$$

where Z_t is the total mortality coefficient, and

R is the total number of recruits in the cohort.

$$N_t = R' e^{[-(F+M)(t-t_c)]}$$
 for $t \ge t_c$

where R' is the number of fish recruiting to the fishery at time $t = t_c$, and therefore,

$$R' = R e^{\left[-Mt_c\right]}$$

Thus the total number caught is:

$$C = \int_{t_c}^{t_L} R' * Fe^{[-(F+M)(t-t_c)]} dt$$
$$= R'(F/(F+M))(e^{[-(F+M)(t_L-t_c)]})$$

or

$$C = R(F/(F+M))(e^{[-M(t_c)]})(1-e^{[(F+M)(t_L-t_c)]})$$

and ignoring the last term if $t_L >> t_c$

$$C = R(F/(F+M))e^{[-M(t_c)]}$$

or

$$C = (F/(F+M))R'$$

Recall that Yield = (Catch)*(Weight), and that the von Bertalanffy growth equation describes individual fish growth as a function of time:

$$W_{t} = W_{\infty} \left[1 - e^{(-Kt)} \right]^{3} = W_{\infty} \left[1 - 3e^{-Kt} + 3e^{-2Kt} - e^{-3Kt} \right]$$

This equation reduces to:

$$W_{t} = W_{\infty} \sum_{n=0}^{3} U_{n} e^{\left(-nKt\right)}$$

where $U_o = 1$, $U_1 = -3$, U_2 , = 3, U_3 , = -1

Incorporating the simplified catch equation and individual fish growth equation into the simplified yield equation results in:

$$Y = F * R e^{[-M(t_c)]} W_{\infty} \sum_{n=0}^{3} \left[U_n e^{(-nKt)} / (F + M + n * K) \right]$$

Yield per recruit is obtained by normalizing the total yield by the number of recruits (R') in the cohort.

Beverton and Holt (1959) noted several important results from the yield per recruit analysis. First is the ratio of the growth parameter (K) to the natural mortality coefficient (M), which estimates the potential of a fish to complete its potential growth before dying of natural mortality.

If M/K is small ($M/K \le 0.5$), then growth is high relative to mortality, and the cohort will reach maximum biomass at a larger size relative to the maximum size, or the stock (in the absence of fishing) will contain relatively larger fish. From a fishery perspective, management should maximum the size or age of entry to the fishery (t_c), with only light fishing mortality on smaller fish.

If M/K is large $(M/K \ge 2.0)$, then natural mortality exceeds growth, indicating many fish will die before completing their potential growth. Again, from a fishery perspective, management should allow heavy fishing with a small size (age) at first capture, so as to harvest the maximum biomass before they die of natural causes.

The yield equation is separated into two parts that characterize the fish stock as a constant and the fishing as a variable. Two additional terms are defined:

Exploitation Ratio
$$E = \frac{F}{(F + M)}$$
, and

Relative Size at First Capture $c = \frac{l_c}{l_{\infty}}$.

The yield equation can then be written as:

$$Y = Y' \left[R * W_{\infty} e^{(-Mt_c)} \right]$$

where

$$Y' = E(1-c)^{(M/K)} \sum_{n=0}^{3} \left[\left(U_n (1-c)^n \right) / 1 + \left(n * K/M \right) (1-E) \right]$$

Beverton and Holt (1957) provide tabulated yield values (Y') for a series of values of M/K from 0.25 to 5.00 for various values of E and c. Tables 1 and 2 illustrate the effect of M/K, c, and E on Y'. Note that for small M/K ratios (0.5), maximum yield is achieved at higher values of c; whereas if M/K is larger (2.0), then maximum yield is achieved at lower values of c.

The Beverton and Holt analytical solution to the yield per recruit (YPR) problem, assuming knife-edge selection, is applied using Tables 1 and 2 or by direct calculation on a computer. With a simple algorithm on a spreadsheet program, a YPR curve is estimated for a particular age or length of entry into the fishery.

					Rate of Exp	loitation												
E = F/(F+M)	0.05	0.10	0.15	0.20	0.25	0.30	0.35	0.40	0.45	0.50	0.55	0.60	0.65	0.70	0.75	0.80	0.85	0.90
L_c/L_{oo}																		
0.98	0.006927	0.013843	0.020748	0.027640	0.034517	0.041379	0.048223	0.055046	0.061845	0.068618	0.075359	0.082063	0.088725	0.095336	0.101887	0.108363	0.114750	0.121024
0.96															0.138356			
0.94															0.162642			
0.92	0.013027	0.025976	0.038837	0.051600	0.064255	0.076788	0.089183	0.101421	0.113482	0.125338	0.136959	0.148306	0.159333	0.169983	0.180184	0.189845	0.198852	0.207056
0.90															0.193199			
0.88	0.015322	0.030503	0.045529	0.060381	0.075040	0.089481	0.103678	0.117598	0.131203	0.144447	0.157277	0.169625	0.181412	0.192539	0.202886	0.212300	0.220591	0.227522
0.86	0.016220	0.032266	0.048119	0.063757	0.079155	0.094284	0.109110	0.123593	0.137686	0.151334	0.164469	0.177012	0.188864	0.199907	0.209992	0.218938	0.226518	0.232453
0.84	0.016997	0.033785	0.050340	0.066637	0.082646	0.098331	0.113652	0.128563	0.143006	0.156915	0.170212	0.182800	0.194565	0.205365	0.215028	0.223343	0.230049	0.234827
0.82	0.017674	0.035102	0.052257	0.069108	0.085621	0.101754	0.117462	0.132687	0.147366	0.161420	0.174759	0.187271	0.198824	0.209255	0.218369	0.225924	0.231628	0.235129
0.80	0.018267	0.036249	0.053916	0.071234	0.088162	0.104653	0.120654	0.136101	0.150920	0.165022	0.178303	0.190638	0.201877	0.211837	0.220297	0.226991	0.231596	0.233733
0.78	0.018787	0.037251	0.055357	0.073066	0.090333	0.107105	0.123321	0.138910	0.153787	0.167855	0.180997	0.193071	0.203911	0.213314	0.221038	0.226790	0.230222	0.230934
0.76	0.019245	0.038127	0.056608	0.074644	0.092185	0.109171	0.125535	0.141198	0.156066	0.170030	0.182961	0.194704	0.205075	0.213853	0.220774	0.225522	0.227727	0.226974
0.75	0.019453	0.038523	0.057171	0.075349	0.093004	0.110076	0.126491	0.142168	0.157009	0.170898	0.183701	0.195256	0.205370	0.213814	0.220313	0.224540	0.226117	0.224623
0.74	0.019648	0.038894	0.057694	0.076001	0.093759	0.110902	0.127356	0.143034	0.157833	0.171635	0.184296	0.195649	0.205493	0.213589	0.219654	0.223351	0.224293	0.222055
0.72	0.020004	0.039565	0.058636	0.077165	0.095089	0.112340	0.128834	0.144476	0.159157	0.172744	0.185086	0.195999	0.205268	0.212638	0.217806	0.220418	0.220073	0.216344
0.70	0.020317	0.040151	0.059450	0.078157	0.096206	0.113520	0.130010	0.145574	0.160092	0.173423	0.185402	0.195834	0.204490	0.211097	0.215337	0.216841	0.215199	0.209988
0.68															0.212341			
0.66															0.208899			
0.64															0.205082			
0.62															0.200953			
0.60															0.196567			
0.58															0.191975			
0.56															0.187220			
0.54															0.182342			
0.52															0.177378			
0.50															0.172357			
0.48															0.167310			
0.46															0.162262			
0.44															0.157236			
0.42															0.152252			
0.40															0.147328			0.095109
0.38															0.142481			
0.36 0.34															0.137725 0.133073			
0.34															0.133073			
0.32															0.128334			
0.28															0.124119			
0.26															0.115686			
0.24															0.111681			
0.24															0.117081			
0.20															0.107822			
0.18															0.104111			
0.16															0.097140			
0.14															0.093880			0.034261
0.14															0.093660			
0.10															0.087801			
0.00															0.075000			
00	022000	2.0.2.50			, 2015			20000		20000			2.100704	2.072040	2.072000		2.02.013	

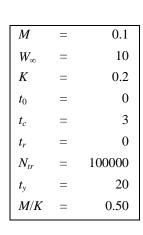
Table 1. Yield per recruit for M/K = 0.5.

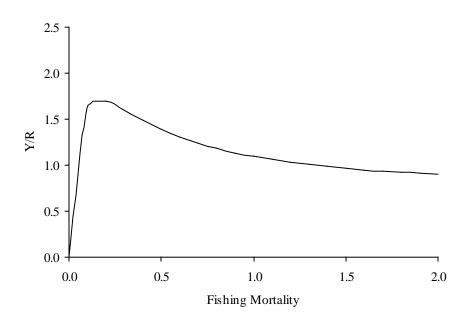
					Rate of Ex	nloitation												
E = F/(F + M)	0.05	0.10	0.15	0.20	0.25	0.30	0.35	0.40	0.45	0.50	0.55	0.60	0.65	0.70	0.75	0.80	0.85	0.90
L_c/L_{oo}				*	***				****	****	****		****		*****			
0.98	0.000019	0.000038	0.000058	0.000077	0.000096	0.000115	0.000134	0.000153	0.000172	0.000191	0.000209	0.000228	0.000247	0.000266	0.000284	0.000303	0.000321	0.000340
0.96						0.000439												
0.94						0.000943												
0.92						0.001600												
0.90						0.002385												
0.88						0.003274												
0.86						0.004246												
0.84	0.000912	0.001812	0.002699	0.003573	0.004434	0.005281	0.006113	0.006929	0.007728	0.008510	0.009274	0.010019	0.010744	0.011448	0.012130	0.012789	0.013424	0.014034
0.82	0.001104	0.002191	0.003261	0.004313	0.005347	0.006360	0.007353	0.008324	0.009273	0.010197	0.011097	0.011971	0.012817	0.013635	0.014423	0.015179	0.015903	0.016592
0.80	0.001303	0.002584	0.003842	0.005076	0.006284	0.007467	0.008622	0.009748	0.010844	0.011909	0.012940	0.013937	0.014898	0.015821	0.016705	0.017549	0.018349	0.019105
0.78	0.001507	0.002985	0.004433	0.005851	0.007235	0.008586	0.009901	0.011179	0.012419	0.013618	0.014774	0.015887	0.016953	0.017971	0.018940	0.019856	0.020719	0.021526
0.76	0.001713	0.003390	0.005029	0.006629	0.008188	0.009704	0.011175	0.012600	0.013976	0.015301	0.016574	0.017791	0.018951	0.020051	0.021090	0.022064	0.022972	0.023813
0.75	0.001816	0.003592	0.005327	0.007017	0.008661	0.010258	0.011806	0.013301	0.014742	0.016127	0.017453	0.018719	0.019920	0.021056	0.022124	0.023121	0.024045	0.024895
0.74	0.001920	0.003795	0.005623	0.007403	0.009132	0.010808	0.012429	0.013993	0.015497	0.016939	0.018316	0.019626	0.020866	0.022033	0.023125	0.024141	0.025077	0.025931
0.72	0.002125	0.004195	0.006209	0.008164	0.010058	0.011888	0.013651	0.015344	0.016966	0.018512	0.019981	0.021369	0.022674	0.023892	0.025021	0.026059	0.027003	0.027852
0.70	0.002327	0.004589	0.006784	0.008908	0.010958	0.012933	0.014828	0.016640	0.018367	0.020006	0.021552	0.023003	0.024356	0.025607	0.026755	0.027796	0.028728	0.029552
0.68	0.002525	0.004973	0.007342	0.009627	0.011826	0.013935	0.015951	0.017871	0.019690	0.021405	0.023014	0.024511	0.025895	0.027161	0.028308	0.029333	0.030234	0.031011
0.66	0.002717	0.005345	0.007879	0.010317	0.012654	0.014887	0.017012	0.019025	0.020923	0.022700	0.024355	0.025882	0.027278	0.028541	0.029668	0.030657	0.031506	0.032218
0.64	0.002903	0.005702	0.008393	0.010974	0.013438	0.015783	0.018004	0.020097	0.022057	0.023881	0.025565	0.027104	0.028495	0.029735	0.030823	0.031756	0.032536	0.033162
0.62	0.003080	0.006042	0.008882	0.011594	0.014174	0.016618	0.018921	0.021079	0.023087	0.024941	0.026636	0.028170	0.029537	0.030737	0.031767	0.032626	0.033316	0.033840
0.60	0.003250	0.006365	0.009341	0.012174	0.014858	0.017388	0.019759	0.021967	0.024007	0.025874	0.027565	0.029074	0.030400	0.031541	0.032495	0.033262	0.033846	0.034251
0.58	0.003410	0.006669	0.009771	0.012712	0.015487	0.018089	0.020514	0.022757	0.024813	0.026677	0.028346	0.029815	0.031082	0.032145	0.033006	0.033665	0.034126	0.034398
0.56	0.003560	0.006952	0.010169	0.013207	0.016059	0.018720	0.021185	0.023447	0.025503	0.027348	0.028978	0.030389	0.031581	0.032551	0.033302	0.033837	0.034162	0.034288
0.54	0.003701	0.007215	0.010535	0.013657	0.016574	0.019279	0.021769	0.024036	0.026077	0.027887	0.029462	0.030800	0.031899	0.032761	0.033388	0.033785	0.033961	0.033930
0.52	0.003831	0.007456	0.010869	0.014062	0.017030	0.019767	0.022266	0.024524	0.026534	0.028294	0.029799	0.031048	0.032041	0.032780	0.033269	0.033516	0.033534	0.033337
0.50	0.003951	0.007677	0.011169	0.014421	0.017427	0.020182	0.022678	0.024911	0.026877	0.028571	0.029992	0.031138	0.032011	0.032614	0.032955	0.033042	0.032892	0.032524
0.48						0.020526												
0.46						0.020801												
0.44						0.021008												
0.42						0.021151												
0.40						0.021232												
0.38						0.021256												
0.36						0.021225												
0.34						0.021144												
0.32						0.021017												
0.30						0.020849												
0.28						0.020645												
0.26						0.020410												
0.24						0.020147												
0.22						0.019863												
0.20						0.019561												
0.18						0.019245												
0.16						0.018921												
0.14						0.018592												
0.12						0.018262												
0.10						0.017934												
0.00	0.004610	0.008445	0.011520	0.013853	0.0154/0	0.016404	0.016696	0.016397	0.015569	0.014286	0.012634	0.010/14	0.008640	0.006539	0.004545	0.002797	0.001421	0.000508

Table 2. Yield per recruit for M/K = 2.0.

Example 1. Consider the development of a harvesting strategy for a roundfish species where K = 0.2, M = 0.1, $W_{\infty} = 10$ kg, and $t_0 = 0$. Should the mesh size in the trawl fishery be regulated to allow entry into the fishery at age 3 or age 5? To what level should fishing mortality be set for these ages so as to maximize yield (F_{MAX}) .

The result of those calculations are illustrated as Figure 1. At a $t_c = 3$, the maximum yield per recruit is 1.70 kg at F = 0.2. In contrast if the $t_c = 5$, the maximum yield per recruit is 2.03 kg at an F = 0.3, an increase of 19%. Interestingly, if t_c is set to 10 years, maximum YPR is achieved at 2.36 kg with an F = 2.0. Thus, for fish species where M/K is small (0.5), substantially greater yields, about 40%, are realized by delaying entry into the fishery.





M	=	0.1
W_{∞}	=	10
K	=	0.2
t_0	=	0
t_c	=	5
t_r	=	0
N_{tr}	=	100000
t_{y}	=	20
M/K	=	0.50

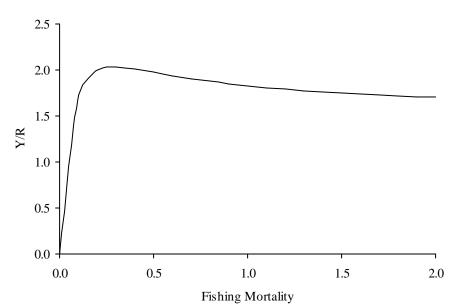


Figure 1. Yield per recruit as a function of fishing mortality;

$$(\mathbf{A})t_c=3.0$$

(B)
$$t_c = 5.0$$
.

Discrete Time Model

A discrete time model (DeAlteris and Riedel, 1996) was developed to incorporate more complex size selection patterns than the knife edge selection assumed in the Beverton-Holt model. The methodology is based on a computer spreadsheet. The time step is set at 0.1 years, over the range of 0 to 30 years.

The length of the fish (L) at age (t) is calculated using a simplified ($t_0 = 0$) von Bertalanffy growth equation:

$$L_{t} = L_{\infty} \left(1 - e^{(-Kt)} \right)$$

where L_{∞} is the maximum length, and K is the instantaneous growth rate.

The weight of the fish (W) at age t is determined using a length-weight relationship.

$$W_{t} = a(L_{t})^{b}$$

where *a* is the *L-W* conversion factor, and *b* is the *L-W* growth factor

The percent maturity (P_t) of individuals in the cohort at age is expressed using a LCDF:

$$P_{t} = (1 + e^{(-\alpha 1 * (t - \beta 1))})^{-1}$$

where αI is the steepness of the curve, and βI is the age at 50% maturity.

The number of individuals (N_t) remaining in the unfished cohort at age t is determined using an instantaneous natural decay function incremented at the time step of t years:

$$N_{t} = N_{(t-1)}e^{\left(-tM\right)}$$

where M is the instantaneous natural maturity, and N_0 , the initial cohort size, is 1000 individuals.

The biomass (B_t) of the individuals remaining in the unfished cohort at age t is calculated:

$$B_t = N_t * W_t$$

and the unfished spawning stock biomass (UFSSB) of the individuals remaining in the cohort at age t is determined:

$$UFSSB_t = P_t * B_t$$

Based on gear selection literature, trawls and hooks are assumed to possess qualitatively similar size selection characteristics, which can be represented by LCDF of individual fish length (PL_t):

$$PL_L = (1 + e^{(-\alpha^2 * (L - L_{50}))})^{-1}$$

where $\alpha 2$ = steepness of the curve, and L_{50} = length at 50% selection.

Gillnets and traps are assumed to possess qualitatively similar size-selection characteristics which can be represented by a truncated, scaled NPDF of individual fish length (PN_t):

$$PN_{L} = e^{\left[-(L-L_{opt})^{2}/(2*SD^{2})\right]}$$

where SD = standard deviation, and L_{opt} = length of maximum selection.

Applying length-specific susceptibility to fishing $(PN_L \text{ or } PL_L)$ at a specified level of fishing mortality (F) and including natural mortality (M), the number of individuals remaining in the fished cohort (NF_t) at each time step (t) is calculated as:

$$NF_{t} = NF_{(t-1)}e^{\{-[((PN_{L}orPL_{L})(F))+M]*t\}}$$

Thus, the yield of the fished cohort (Y_t) from each time-step is:

$$Y_{t} = \left[\begin{array}{cccc} (PN_{L} & or & PL_{L})(F) / \\ / ((PN_{L} & or & PL_{L})(F)) + M \end{array} \right] * (NF_{(t-1)} - NF_{t}) * (W_{t})$$

and the spawning stock biomass of the fished cohort (SSB_t) at each time step is simply:

$$SSB_t = (NF_t)*(W_t)*(P_t)$$

Given these equations and specific values of L_4 , K, a, b, $\alpha 1$, $\beta 1$, and M, the total biomass and spawning stock biomass of the unfished cohort are determined. With the specification of fishing conditions (F, $\alpha 2$, L_{50} , SD, and L_{opt}) total yield and spawning stock biomass of the fished cohort are determined. By evaluating a wide range of L_{50} , L_{opt} and F values, the resulting matrix of data, expressed as a percentage of the maximum value, is contoured to produce isopleth diagrams of yield per recruit (YPR) and spawning stock biomass per recruit (SPR).

The effect of the selectivity function's shape on YPR and SPR is evaluated by specifying a range of steepness and standard deviations for the LCDF and NPDF while holding other factors constant.

Example 2. Evaluate the effects of increasing size at entry from 50 to 100 cm in 10 cm increments on the yield and SSB of an idealized roundfish harvested by both trawls and gill nets. For trawls, the steepness of the LCDF curve is 0.33. For gill nets, the standard deviation of the NPDF is 5. The specifications for the idealized roundfish used in this analysis are: $L_{\infty} = 100$ cm, $W_{\infty} = 10$ kg, K = 0.2, a = 0.00001, b = 3, a1 = 1, b2 = 3, and b2 = 0.2.

Based on these values, the characteristics of the individuals and the cohort of idealized roundfish are shown in Figures 2 and 3. An individual idealized roundfish reaches an asymptotic maximum length and weight of 100 cm and 10 kg. Maturation is assumed to occur rapidly, with 50% of the cohort mature at an age of 3 years and a length of about 45 cm. Based on an initial cohort of 1000, the number of individuals in the unfished cohort is reduced to about 5% of the initial number by the age of 16 years, although the model is extended to an age of 30 years when only a single fish remains. Biomass of the cohort peaks at an age of 6.3 years and an individual fish length of 75 cm.

The LCDF and NPDF for size selection are shown in Figures 4A and 4B. The L_{50} s for the LCDF ranged from 50 to 100 cm, and a representative steepness of 0.33 is specified. The L_{opt} s ranged from 50 to 100 cm, and a representative standard deviation of 5 is specified.

The spreadsheet program is now run for a range of fishing mortality values from 0 to 0.5 at 0.1 intervals and 0.5 to 4.0 at 0.5 intervals, calculating YPR and SPR values for both types of selection functions at each of the six L_{50} and L_{opt} values. The resulting isopleth diagrams for YPR and SPR are shown in Figures 5 and 6 for the LCDF and NPDF, respectively.

Evaluating the isopleth diagrams for the LCDF, it is clear that maximum YPR will be realized at an L_{50} of 80 cm and at fishing mortalities of 3.0 and greater. Operating the fishery in this range will provide a relative SPR of 35% at F = 3.0, decreasing to 25% at F = 4.0.

Evaluating the isopleth diagrams of the NPDF, it is clear again that maximum YPR will be realized at a L_{50} of 80 cm and at fishing mortalities of 2.0 and greater. Operating the fishery in this range will provide a spawning stock biomass of 30% at F = 2.0, decreasing to 26% at F = 4.0.

The effect of the shape of the selection curve on the YPR and SPR is evaluated at an L_{50} or L_{opt} of 80 cm and an F value of 3.0. Steepness values ranging from 0.13 to 2.00 are specified for the LCDF (Figure 7). Increasing the steepness of the selection curve effects both the YPR and SPR. Lower values for the steepness parameter results in a 100% increase in YPR and 50% reduction of the SPR. Standard deviation values ranging from 2 to 10 are specified for the NPDF (Figure 8). Increasing the standard deviation of the selection curve results in 50% reduction in SPR and a 300% increase in YPR.

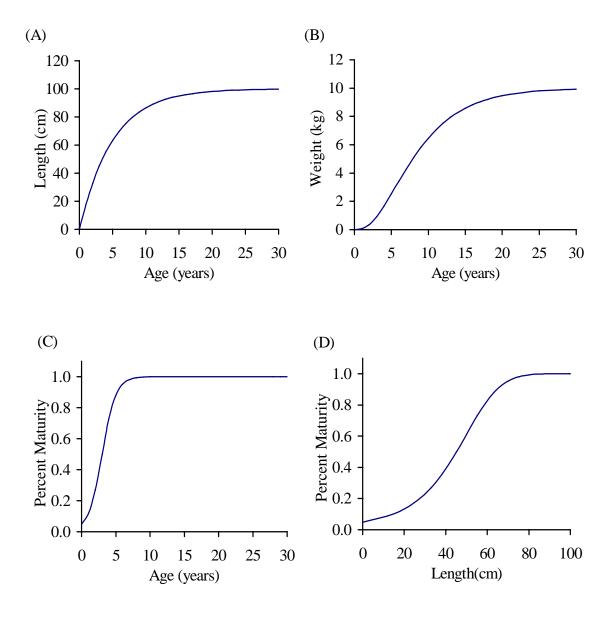


Figure 2. Functional characteristics of an unfished cohort of an idealized roundfish;

- (A) Length as a function of age
- (B) Weight as a function of age
- (C) Percent Maturity as a function of age
- (D) Percent Maturity as a function of length.

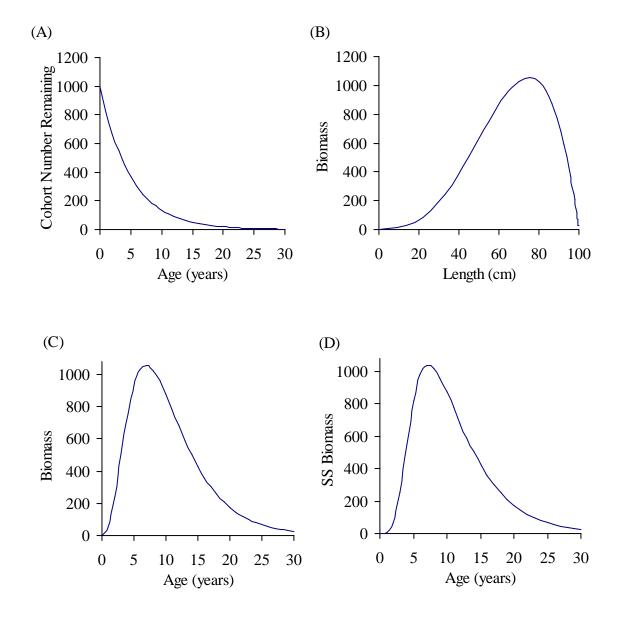


Figure 3. Functional characteristics of an unfished cohort of an idealized roundfish;

- (A) Numbers as a function of age
- (B) Biomass as a function of length
- (C) Biomass as a function of age
- (D) Spawning Biomass as a function of age.

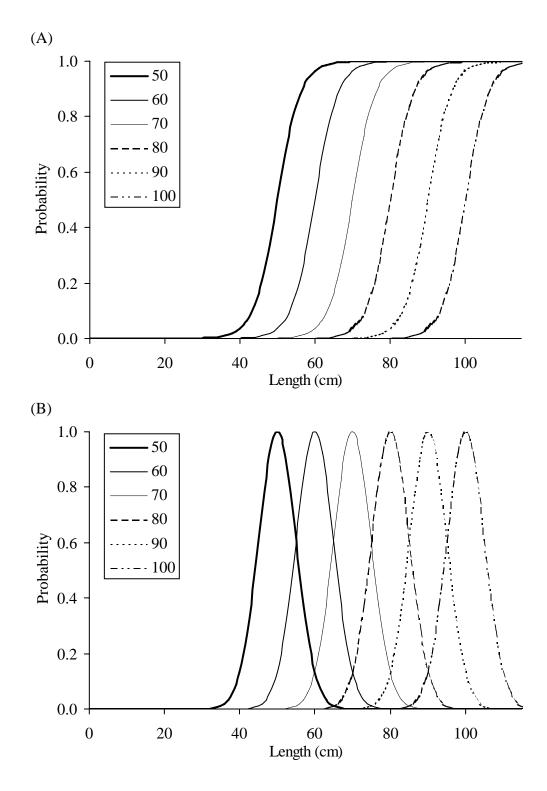


Figure 4. Selection characteristics of harvesting gears used on the cohort of idealized roundfish; (A) Logistic cumulative distribution function (LCDF) selectivity curves for L_{50} s from 50-100 cm

(B) Normal probability density function (NPDF) selectivity curves for $L_{\rm opt}$ s from 50-100 cm.

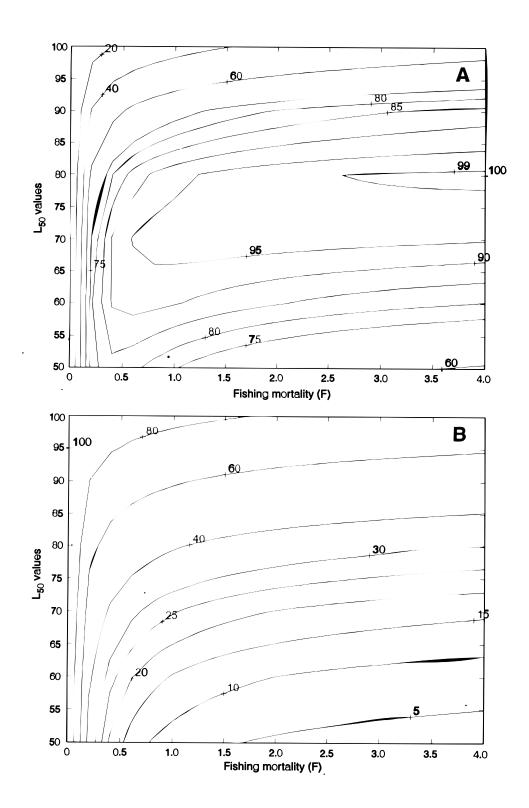


Figure 5. Isopleth diagrams expressed as a percentage of maximum for size selection based on a LCDF: (A) Yield per Recruit (YPR), and

(B) Spawning stock biomass per recruit (SSBPR).

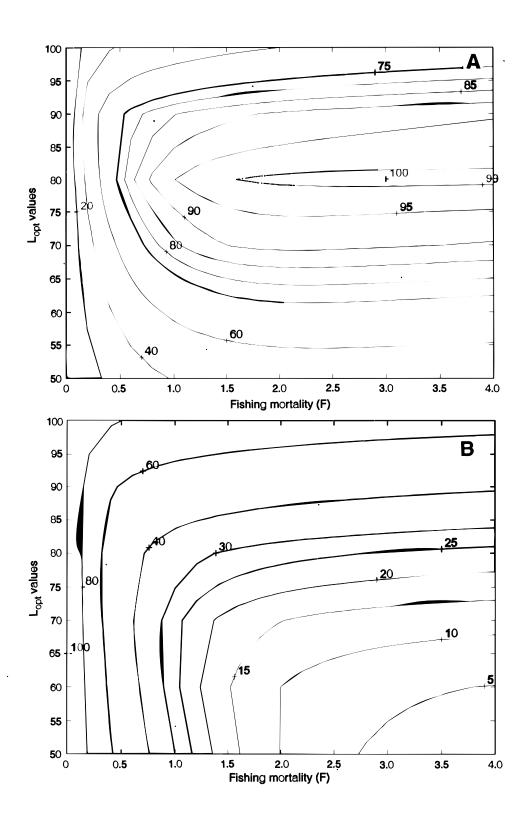
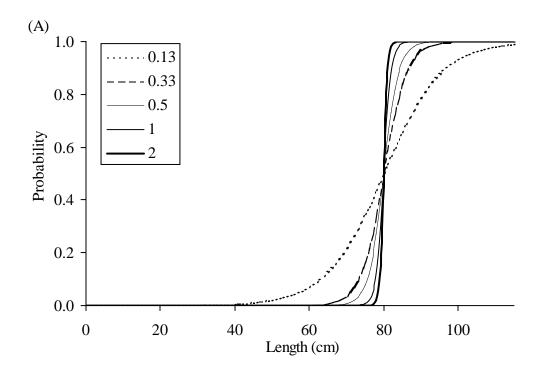


Figure 6. Isopleth diagrams expressed as a percentage of maximum for size selection based on a NPDF: (A) Yield per recruit (YPR), and

(B) Spawning stock biomass per recruit (SSBPR).



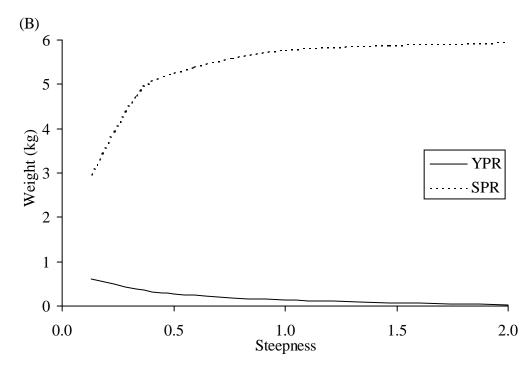
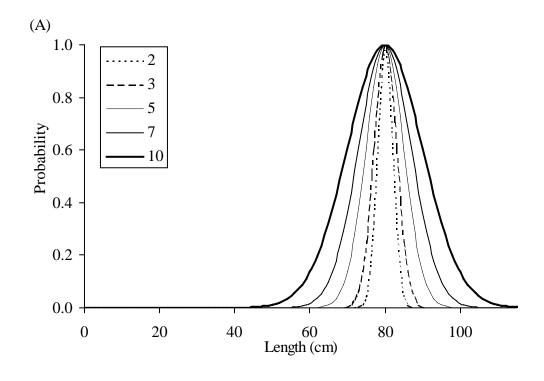


Figure 7. Effect of the steepness of the LCDF on the cohort of an idealized roundfish: (A) Size selectivity curve, and (B) YPR and SPR at $L_{50} = 80$ cm and F = 3.0.



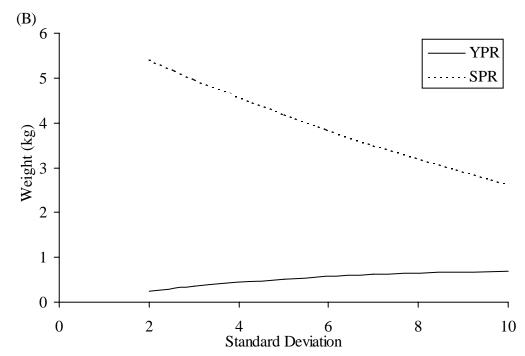


Figure 8. Effect of the standard deviation of the NPDF for the cohort of an idealized roundfish: (A) Size selectivity curve, and

(B) YPR and SPR at $L_{opt} = 80$ cm and F = 3.0.

Exercises

Northwest Atlantic groundfish species have markedly different growth and mortality rates as indicated in the following table.

Species	K	M	M/K	W_{∞}	L_{∞}
cod	0.12	0.2	1.7	33.7	148
haddock	0.38	0.2	0.5	4.4	74
silver hake	0.18	0.4	2.2	2.0	65
winter flounder	0.37	0.2	0.5	3.5	63
yellowtail flounder	0.63	0.2	0.3	0.9	46
plaice	0.17	0.2	1.2	2.4	65
summer flounder	0.21	0.2	1.0	7.6	84

Given this variability in M/K ratios and L_{∞} , there is the need to have different harvesting strategies in terms of age at entry into the fishery and target fishery mortality levels to maximize yield. The implementation of these strategies requires differing mesh size regulations for a trawl fishery so as to control age at entry, or retention by the gear.

- 1. Using the Beverton-Holt analytical solution to the yield per recruit problem, compare the harvesting strategies (age at entry to the fishery, and fishing mortality) to maximize yield for cod, silver hake and yellowtail flounder. Note that silver hake and cod have a M/K ratio of about 2.0, while yellowtail flounder has a M/K ratio of less than 0.5. Assuming that the selection factor for diamond mesh trawl codends are 3.7, 3.5, and 2.6 for cod, silver hake, and yellowtail flounder, respectively, and that management seeks to match trawl selection (L_{50}) to YPR_{MAX} , targets, determine the appropriate mesh size for each species. Recall that the simplified von Bertalanffy age-length relationship is $L_t = L_{\infty} \left(1 e^{[-K*t]}\right)$.
- 2. Using the discrete YPR and SSB model for summer flounder, compare the yield and spawning stock biomass curves for gillnets and trawls if gear regulations are set so as to achieve L_{50} s and L_{opt} s, of 35 cm as in the present regulations, and 55 cm as may be a future target.

Notes

- A. Summer flounder maturity parameters are $\alpha I = 5$ and $\beta I = 2.37$ and length-width relationship parameters are a = 0.0001, and b = 3.07.
- B. NPDF SD is 5, and the LCDF steepness 0.33.
- C. Develop the discrete time YPR and SSB per recruit curves at *F* intervals of 0.1 in the range of 0.0 to 0.5, and intervals of 0.5 in the range of 0.5 to 3.0.
- D. When evaluating the SSB curve, note the 20% of virgin SSB line.

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Chapter VII

SURPLUS PRODUCTION MODELS

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Introduction

Thus far, the growth and mortality of a single cohort of animals has been considered. Based on species-specific life history characteristics, a model for a harvesting strategy that includes age at entry into the fishery and a fishing mortality rate has been derived for a cohort of animals. The yield per recruit (YPR) analysis is used to set targets or reference points for the harvest of a fishery resource to maximize yield and prevent growth overfishing. The corollary to the YPR analysis is the spawning stock biomass or egg per recruit analysis that is used to ensure that a minimum percentage of the virgin spawning stock biomass or egg production remains in the stock, so as to prevent recruitment overfishing. While these analyses are useful to set harvesting targets assuming a healthy stock and consistent recruitment to that stock, clearly the intensity of fishing must also be regulated with respect to the status of the stock, that is the abundance of animals in the stock relative to maximum number of animals of a particular species that the ecosystem can support. This concept is fundamental in ecology and refers to the carrying capacity of the environment.

There are two broad categories of models used to assess that status of fish stocks:

- 1. Global models, known as production or biomass dynamic models which do not distinguish between recruitment, growth, and mortality as contributing factors to overall changes in population abundance but consider only their resultant effect as a single function of the population size. These models do not rely on age structure, and are particularly useful when age data is not available or when the catch cannot be aged. These models are simple in their concept and use, and require a minimum of data.
- 2. Structural models, known as age-structured models include cohort analysis or virtual population analysis, which divide the catch into age groups and provide estimates of time specific biomass and fishing mortality at age. These models require more data and can be complicated when allowing calibration using independent information on abundance-at-age of the stock.

This chapter develops the concepts and application of global models, which include the surplus or stock production models that assume quasi-equilibrium conditions between yield and effort. These models are the precursors of the true biomass dynamic models that consider time-history trends in biomass indices and catch.

Population Growth and Regulation

The simplest model of population growth over time assumes birth (*b*) and death (*d*) rates are consistent over all ranges of population density (*i.e.* these rates are density independent). Assuming that the population is closed, spatially homogeneous, and that there is no age structure, the time history of that population is described by:

$$\frac{dN}{dt} = (b-d)N = rN$$

where r is the intrinsic rate of growth or decay of the population.

If the birth rate exceeds death rate, then dN/dt is positive (r > 0); if the birth rate equals death rate then dN/dt is zero (r = 0); and if death rate exceeds the birth rate, then dN/dt is negative (r < 0). Note that this relationship is a differential equation, but it also fits the linear model y = ax (Figure 1).

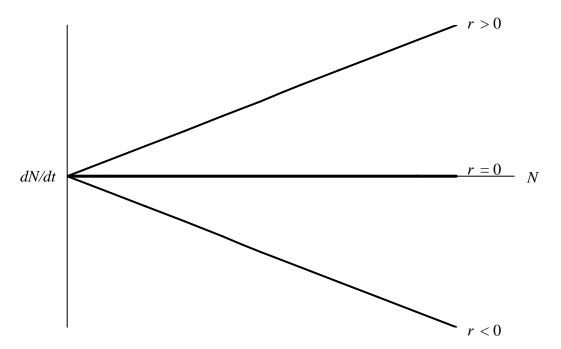


Figure 1. The rate of change of population number (dN/dt) as a function of population size (N) for r > 0, = 0, and < 0.

Note also that if the differential equation is rearranged as follows:

$$\left(\frac{1}{N}\right) dN/dt = (b-d) = r$$
.

The "per capita" rate of change of a population in this density independent model is a constant (r).

This differential equation is solved by the separation of variables method,

$$\int \frac{1}{N} dN = \int (b-d) dt$$

$$N_t = N_0 e^{(b-d)t}.$$

The trajectory of a population with density independent birth and death rates is shown in Figure 2. If r > 0, then population numbers grow exponentially; if r < 0, population numbers decay as a negative exponential to 0, and if r = 0 the population remains in a neutral equilibrium, where any perturbation will disturb the balance, and the population will grow exponentially or decline toward extinction.

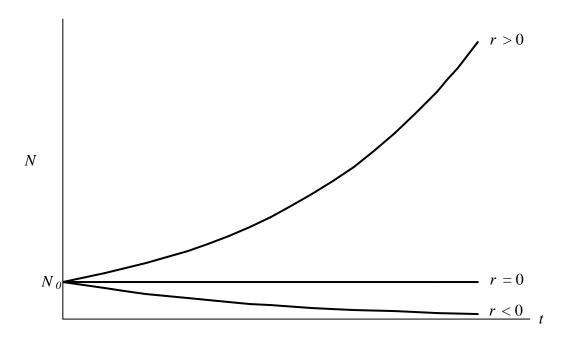


Figure 2. Population trajectories for density independent growth where r > 0, = 0, and < 0.

In summary, while a model that includes only density independent terms is conceptually simple, it is incapable of producing a stable population. Therefore, density dependence must be introduced into the model to regulate population growth.

A reasonable approach for the addition of density dependence in the birth and death rates is to express these as linear functions:

$$b = b_0 - b_1 N$$
$$d = d_0 + d_1 N$$

where b_0 and d_0 are the rates at N = 0, and

 b_1 and d_1 are the population dependent coefficients.

These functional relationships are shown in Figure 3, and are incorporated into the basic population growth equation as follows:

$$\frac{dN}{dt} = [(b_0 - b_1 N) - (d_0 - d_1 N)]N$$

or rearranging:

$$dN/dt = [(b_0 - d_0) - (b_1 + d_1)N]N$$
.

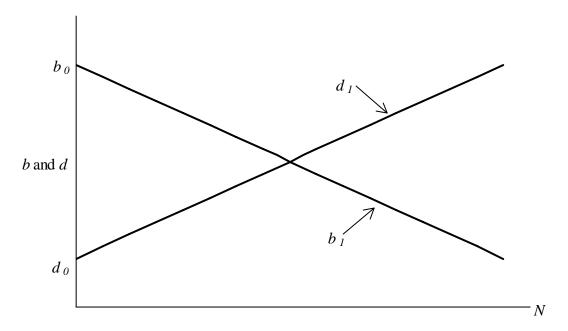


Figure 3. Birth (b) and death (d) rates incorporating density dependence.

Replacing the initial birth and death rate difference with α and the density dependent birth and death rate coefficients with β results in the following:

$$\frac{dN}{dt} = (\alpha - \beta N)N = \alpha N - \beta N^{2}.$$

Note that this equation has the form of a parabolic function (Figure 4). Additionally,

at
$$N = 0$$
, $\frac{dN}{dt} = 0$

at
$$N_{\text{MAX}}$$
, $\frac{dN}{dt} = 0$

$$N_{\text{MAX}} = \alpha / \beta = \frac{(b_0 - d_0)}{(b_1 + d_1)}$$

and the population size (N) that achieves the maximum rate of population change is determined by taking the derivative of the function and setting it equal to zero:

$$\frac{d}{dN}[(\alpha - \beta N)N] = 0$$

$$\alpha - 2\beta N = 0$$

$$N = \frac{1}{2} \left(\frac{\alpha}{\beta}\right) \text{ or } \frac{1}{2} \text{ carrying capacity.}$$

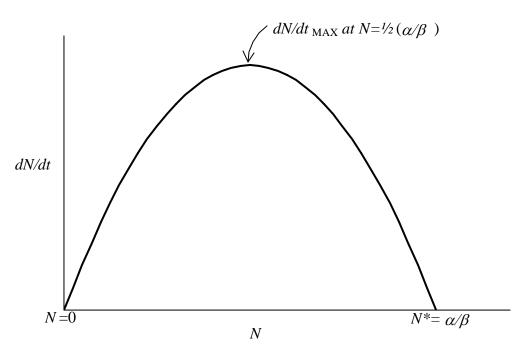


Figure 4. Parabolic model relating density dependent rate of population change to population size.

The differential equation relating $\frac{dN}{dt}$ to N is solved using the separation of variables method:

$$\int \left[\frac{1}{(\alpha-\beta N)N}\right] dN = \int dt$$

$$N_{t} = \frac{[\alpha/\beta]}{[((\alpha-\beta N)/\beta N_{0})e^{-\alpha t} + 1]}$$
substituting
$$N_{MAX} = \left(\frac{\alpha}{\beta}\right)$$
and
$$\gamma = \frac{(\alpha-\beta N_{0})}{(\beta N_{0})}$$
yields:
$$N_{t} = \frac{N_{MAX}}{[1+\gamma e^{-\alpha t}]}.$$

Note that this equation has the form of a generalized logistic function (Figure 5).

carrying capacity =
$$k$$

$$N* = \alpha/\beta$$

Figure 5. Logistic model describing population number as a function of time.

Anthropogenic mortality or harvesting is added to the model of population regulation as follows:

$$dN/dt = (\alpha - \beta N)N - aN$$

where a is a coefficient or rate of anthropogenic removal that can be equated to a fishing mortality rate.

Surplus Production Model

Russell (1935) advanced the mass-balance concept, arguing that fish stocks fluctuate in abundance according to imbalance between additions and losses to the stock and this balance can be summarized as follows:

New Biomass = Old Biomass + Recruitment + Growth - Catch - Natural mortality.

If the sum of the recruitment and growth is larger than the sum of catch and natural mortality, a stock increases in abundance; if the losses exceed the additions, the stock declines. Grouping terms relating to natural processes (recruitment, growth, and natural mortality) and referring to them collectively as *Surplus Production* yields:

New Biomass = Old Biomass + Surplus Production - Catch.

For a stock to remain at a given level of biomass (New Biomass = Old Biomass), the fishery removal (catch) should not be larger than the surplus production of the stock. To rebuild a stock, catch must be lower than the surplus production.

These types of models are attractive in stock assessment in that not only do they have biological soundness but also require minimal amounts of data. The basic set of data required for surplus production models is a time series of catch and fishing effort.

Schaefer Model

The surplus production model is derived from the density dependent population growth model by replacing population number (N) with biomass (B),

$$dB/dt = (\alpha - \beta B)B - FB$$
.

At equilibrium $\frac{dB}{dt} = 0$, therefore:

$$(\alpha - \beta B^*)B^* = F^*B^*$$
$$(\alpha - \beta B^*) = F^*$$
$$B^* = (\alpha - F^*)/\beta$$

where B^* represents equilibrium levels of biomass at specific equilibrium levels of fishing mortality (F^*) .

Recalling that catch or anthropogenic removal is the product of biomass and fishing mortality then equilibrium yield values are defined as:

$$Y^* = F^* B^*.$$

Substituting for equilibrium biomass and expanding results in the basic surplus production model:

$$Y^* = F^* \left(\frac{\alpha - F^*}{\beta} \right) = \left[\left(\frac{\alpha}{\beta} \right) - \left(\frac{1}{\beta} \right) F^* \right] F^*.$$

Substituting:

$$a \text{ for } \left(\frac{\alpha}{\beta}\right)$$

 $b \text{ for } \left(\frac{1}{\beta}\right), \text{ and }$

f for F assuming catchability is constant (based on F = fq)

results in the generalized Schaefer Model (1954):

$$Y = (a - bf)f = af - bf^{2}.$$

This model has the parabolic or dome shaped form that relates yield (Y) to fishing effort (f) (Figure 6). The level of effort required to achieve Maximum Equilibrium Yield (MEY) is determined by taking the derivative of the function and setting it equal to zero:

$$\frac{d}{df} \left[af - bf^{2} \right] = 0$$

$$a - 2bf = 0$$

$$f_{MEY} = \frac{a}{2b}.$$

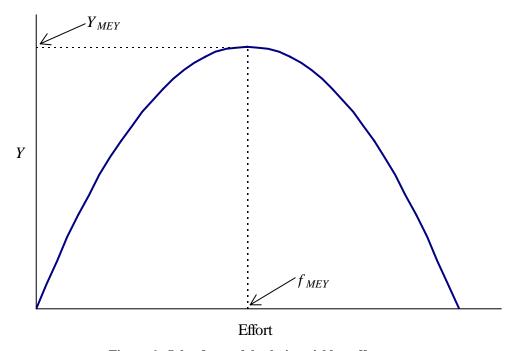


Figure 6. Schaefer model relating yield to effort.

MEY is then determined by substituting f_{MEY} back into the original equation:

$$Y_{MEY} = a \left(\frac{a}{2b} \right) - b \left(\frac{a}{2b} \right)^{2}$$

$$= a^{2} \left(\frac{ba^{2}}{4b^{2}} \right)^{2}$$

$$Y_{MEY} = 2a^{2}b \left(\frac{a^{2}b}{4b^{2}} - \frac{a^{2}b}{4b^{2}} \right) = a^{2}b \left(\frac{a^{2}b}{4b^{2}} \right)^{2} = a^{2}b \left(\frac{a^{2}b}{4b^{2}} \right)^{2}$$

Notice that the MEY occurs at the point of maximum growth (one-half carrying capacity).

The parameters a and b of the Schaefer model are initially estimated by linearizing the function:

$$Y/f = a - bf$$
,

and using linear regression on CPUE $\binom{Y}{f}$ versus effort (f). Non-linear, best-fit estimation of the parameters is accomplished using **Solver** in *Microsoft Excel*, with parameter starting values from the linearized estimation.

Fox Model

An alternative model to fitting the relationship between catch and effort was introduced by Fox in 1970 which assumes that a stock would respond to intense fishing by maximizing productivity thus the yield would never reach zero. This model also assumes that CPUE would decline as effort increases and provides an estimate of the MEY usually close to the Schaefer model. The Fox model has the form

$$Y = fe^{(c-df)}.$$

This model is linearized to:

$$\ln\left(\frac{Y}{f}\right) = c - df$$
.

MEY for the Fox model is estimated by again taking the derivative of the function, setting it equal to zero to solve for f at MEY, and finally, substituting that back into the original equation:

$$f_{MEY} = \frac{1}{d}$$

$$Y_{MEY} = \left(\frac{1}{d}\right) e^{(c-1)}.$$

Example 1: Consider the following time series of catch and effort for a trawl fishery. Determine the MEY for this fishery by fitting the Schaefer and Fox models. Recommend a level of effort to achieve MEY.

Year	Catch	Effort
1988	50	623
1989	49	628
1990	47.5	520
1991	45	513
1992	51	661
1993	56	919
1994	66	1158
1995	58	1970
1996	52	1317

1. The time history of the catch and effort data is shown in Figure 7.



Figure 7. Time history of catch and effort.

2. To fit the linearized Schaefer model, calculate CPUE as ratios of catch/effort (Table 1), then use linear regression of CPUE versus effort (Figure 8).

Table 1. Trawl catch and effort data with CPUE.

Year	Catch	Effort	CPUE
1988	50	623	0.080257
1989	49	628	0.078025
1990	47.5	520	0.091346
1991	45	513	0.087719
1992	51	661	0.077156
1993	56	919	0.060936
1994	66	1158	0.056995
1995	58	1970	0.029442
1996	52	1317	0.039484

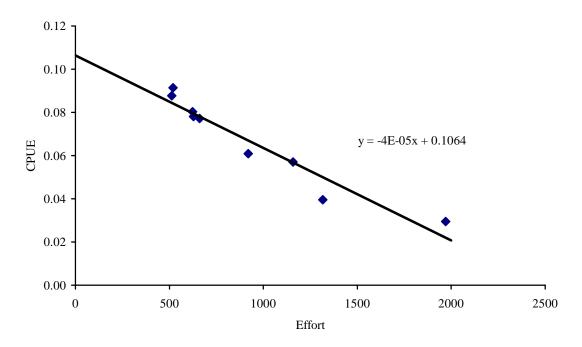


Figure 8. Linearization of the Schaefer model and the best fit regression.

- 3. Using the *a* and *b* coefficients from the linear regression as starting values, use **Solver** to fit the non-linear model (Figure 9). (Note the Sum of the Squared Residuals (SSR).)
- 4. Using the best fit coefficients, estimate MEY and the recommended level of effort to achieve MEY.
- 5. To fit the linearized Fox model, determine the ln(CPUE) (Table 2), and then linearly regress ln(CPUE) versus effort (Figure 10).

Table 2. Trawl catch and effort data with the ln(CPUE).

Year	Catch	Effort	ln(CPUE)
1988	50	623	-2.52252
1989	49	628	-2.55072
1990	47.5	520	-2.39310
1991	45	513	-2.43361
1992	51	661	-2.56193
1993	56	919	-2.79793
1994	66	1158	-2.86479
1995	58	1970	-3.52535
1996	52	1317	-3.23187

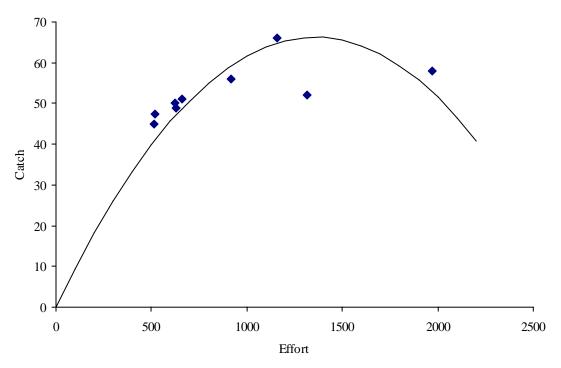


Figure 9. Non-linear Schaefer model best fit to the catch and effort data.

- 6. Using the *c* and *d* coefficients from the linear regression as starting values, use **Solver** to fit the non-linear model (Figure 11). (Note the Sum of Squared Residuals (SSR).)
- 7. Using the best fit coefficients, estimate the MEY and recommend level of effort to achieve MEY.

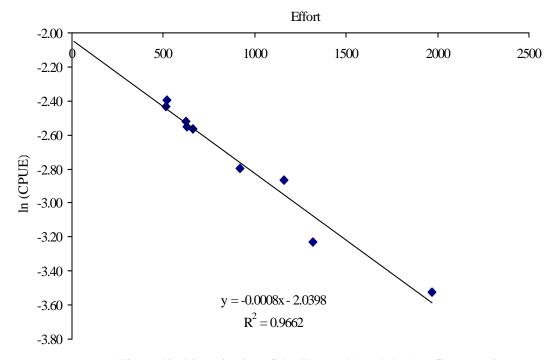


Figure 10. Linearization of the Fox model and the best fit regression.

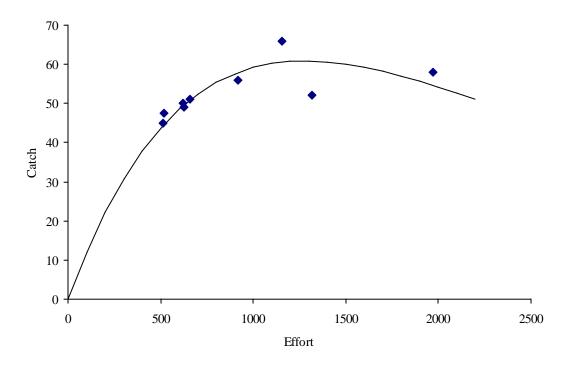


Figure 11. Non-linear Fox model best fit to the catch and effort data.

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Exercises

Given the following catch and effort data for the trawl fishery on this pelagic fish species for the period 1976 to 1995,

Year	Catch (10 ⁶ kg)	Effort (10,000 days)
1976	104	0.13
1977	282	0.28
1978	348	0.39
1979	507	0.51
1980	548	0.72
1981	602	0.98
1982	584	1.12
1983	542	0.96
1984	521	1.03
1985	487	1.09
1986	472	1.15
1987	416	1.22
1988	298	1.32
1989	150	1.50
1990	72	1.52
1991	81	1.53
1992	60	1.56
1993	82	1.58
1994	75	1.60
1995	71	1.62

- A. Plot the trajectories of catch and effort. Describe the time history of the fishery.
- B. Estimate the parameters of Schaefer and Fox Surplus Production models for the data using linear regression.
- C. Use **Solver** to improve the parameter estimates for the Schaefer and Fox models.
- D. Estimate Y_{MEY} and f_{MEY} for both models, compare graphic and empirical estimates.

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Chapter VIII

STOCK AND RECRUITMENT

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Introduction

Recruitment processes include those factors that affect the growth and survival of fish between the egg and the age that fish enter either the spawning stock biomass portion of the population or become vulnerable to harvesting. Consider a basic two-stage life history model for fish:

$$\begin{array}{c}
\xrightarrow{F+M} \\
 & \xrightarrow{\text{ADULTS.}} \\
 & \xrightarrow{\text{RECRUITMENT}}
\end{array}$$

Recruits, having entered the fishery, are subject to the fishing (F) and natural mortality (M), and once mature contribute to egg production before being harvested or dying of natural causes. Eggs must hatch, releasing larvae that metamorphose into juvenile fish which must survive to the recruit stage. The development and survival of the egg, larval, and juvenile life stages are affected by predation, genetic fitness, nutrition, and environmental factors.

The purpose of investigating stock-recruitment (*S-R*) relationships for fishery resources is to be able to predict the number of recruits to the fishery at a future date based on estimates of the present spawning stock abundance. In reality, stock-recruitment relationships are used by resource managers as a rationale for regulating fishing mortality so as to avoid low stock sizes that may lead to recruitment failure and stock collapses.

Biological Processes

Density independent mortality in the stock-recruitment relationship implies that the probability of eggs surviving to the recruit stage is independent of the spawning stock size or number of eggs produced. Biologically, this is a simple and reasonable assumption, but within limits. No population can reproduce with the same average probability of success as stock size increases indefinitely. Eventually, every population becomes limited by resources available. Compensation is the reduction in recruits-per-spawner as spawning stock size increases. The result is that the *S-R* curve rises less steeply at higher stock sizes, asymptotes, and can eventually fall off at the highest stock levels. Density dependent factors include maturation and fecundity, growth, predation, and cannibalism. Depensation is an increase in recruits-per-spawner as spawning stock increases.

Measurement of Spawning Stock and Recruitment

Spawning stock is measured by the following:

- 1. Number of females alive at each age times fecundity at age,
- 2. Number of individuals alive at each age times fecundity at age,
- 3. Total biomass of individuals at or above the age of first reproduction, and
- 4. Index and abundance of the population in the year eggs are deposited.

Recruitment is measured by the following:

- 1. Recruits to the fishery determined by Virtual Population Analysis (VPA) from catch-at-age data and
- 2. Juvenile / pre-recruit surveys.

Basic Principles of the S-R Relationship

Ricker (1975) proposed some basic tenets for the S-R relationship:

- 1. The curve must start at the origin, that is at S(0), R(0).
- 2. At no point after S(0) will there be a R(0) (*i.e.* at high densities recruitment will not go to zero).
- 3. The rate of recruitment (R/S) should decrease continuously with increasing stock size; that is the highest rate of recruitment should be at the lowest stock level.
- 4. Recruitment must exceed parental stock size over some part of the range of *S* (when *R* and *S* are in the same units), otherwise stock collapse would result from any perturbation to the system.

Beverton-Holt Model

The Beverton-Holt *S-R* relationship (1957) is based on the assumption that juvenile competition results in a mortality rate that is linearly dependent upon the number of fish alive in the cohort at any time.

$$dN/dt = -(q + pN)N$$

where N is the number alive in the cohort at time t,

q is a density-independent mortality rate, and

pN is a mortality rate component that is proportional to the density of the cohort at time t.

The Beverton-Holt S-R relationship is asymptotic. If R and S are in the same units and R = S at replacement (S_r), then:

$$R = S / \left[1 - A \left(1 - \frac{S}{S_r} \right) \right]$$

where *A* is the shape of the curve and has values of $0 \rightarrow 1$ (Figure 1).

If R and S are in different units, then:

$$R = 1 / \left(\alpha + \frac{\beta}{S}\right) = \frac{S}{\alpha S + \beta}$$

where $\beta = 1$ -A and $\alpha = A/S_r$.

Note that as $S \to \infty$, $R = 1/\alpha$.

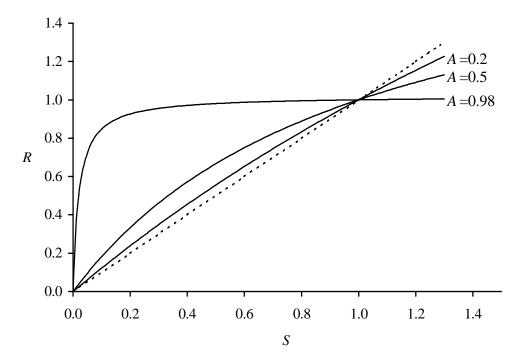


Figure 1. The Beverton-Holt S-R relationship with changing values of A.

Ricker Model

The Ricker *S-R* relationship (1954, 1975) is based on the assumption that the mortality rate of eggs and juveniles is proportional to the initial cohort size. In other words, mortality is spawning stock dependent rather than cohort size dependent as in the Beverton-Holt model.

$$dN/dt = -(q + pS)N$$

where N is the cohort size at any time prior to recruitment, S is the initial spawning stock size, q is the density independent mortality rate, and (q + pS) is the mortality rate for the cohort.

The Ricker model

$$R = \alpha S e^{-\beta S}$$

where α is the recruits per spawners (R/S, the slope) at low stock sizes, and β is the shape of the curve

results in recruitment declining at high stock levels (Figure 2).

When spawning stock and recruits are measured in the same units, the replacement level (R = S) and $S_r = \ln \alpha/\beta$.

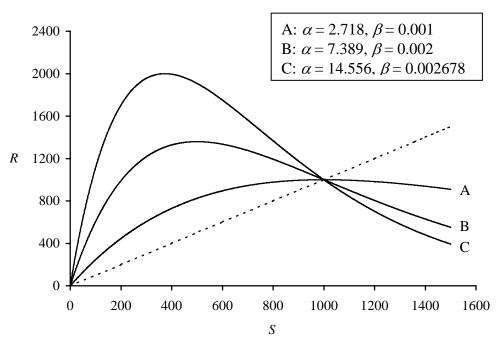


Figure 2. The Ricker S-R relationship at various α and β values.

Shephard Model

The Shepherd *S-R* relationship (1982) is a more versatile form of the *S-R* (Figure 3). It can accommodate both the Beverton-Holt and Ricker *S-R* relationships:

$$R = \alpha S / \left[1 + \left(S / K \right)^{\beta} \right]$$

where α is the slope at the origin,

 β describes the shape of the curve and provides for the degree of compensation, and K is the threshold stock biomass above which density dependent effects overcome density independent effects.

The degree of compensation (β) measures the power of the density dependent effects to compensate for changes of stock size. If $\beta < 1$, recruitment continues to increase when biomass increases, indefinitely. If $\beta = 1$, then at large stock sizes density dependent effects compensate

exactly for increases in biomass, leading to asymptotically constant recruitment. If $\beta > 1$, the density dependent processes are so strong that they over-compensate for changes in biomass, leading to decreased recruitment at higher stock sizes. The threshold biomass (K) is the biomass at which recruitment is reduced to half the level it would have had under density-independent process alone.

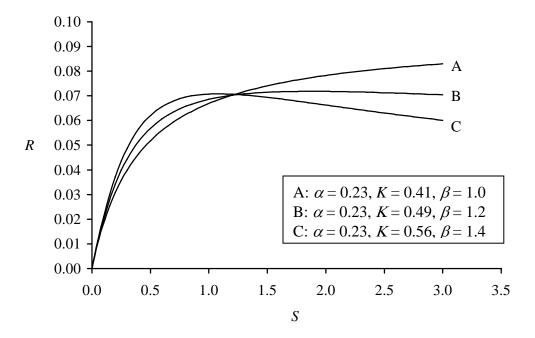


Figure 3. The Shepard S-R relationship at various α , K, and β values.

Estimation of S-R Parameters

The general form of Beverton-Holt model can be rearranged as follows:

$$R = \frac{1}{\left[\alpha + \frac{\beta}{S}\right]} = \frac{S}{\alpha S + \beta}$$
$$\frac{S}{R} = \beta + \alpha S.$$

In the rearranged form, the Beverton-Holt *S-R* relationship conforms to the basic linear model:

$$y = ax + b$$

where
$$y = S/R$$

 $a = \text{slope} = \alpha$
 $x = S$
 $b = \text{intercept} = \beta$.

The α and β parameters are estimated by regressing S/R against S. These values are then used to plot a predicted Beverton-Holt S-R curve, or can be used as starting values for non-linear regression methods.

Example 1: Given the following stock recruitment data, solve for α and β using both the linear and non-linear methods of the Beverton-Holt model.

Year	Stock	Recruitment	S/R
1	8.8	7.1	1.239
2	7.4	6.4	1.156
3	4.5	6.4	0.703
4	13.2	7.0	1.886
5	14.6	7.7	1.896
6	7.0	7.0	1.000
7	3.1	5.4	0.574
8	7.7	6.1	1.262
9	10.7	6.8	1.574
10	8.6	6.0	1.433
11	15.4	6.2	2.484
12	2.0	3.5	0.571

The data are fit to a linear model using a regression of S/R versus S (Figure 4). The values of α and β are obtained directly from the slope and y-intercept values where $\alpha = a$ and $\beta = b$. Therefore, $\alpha = 0.1319$ and $\beta = 0.1824$. Nonlinear regression is performed using **Solver** in *Microsoft Excel* and the linear regression parameter values as starting values. The new parameter values are $\alpha = 0.1262$ and $\beta = 0.2167$. The Beverton-Holt model is graphed onto the original data using the non-linear regression parameter values (Figure 5).

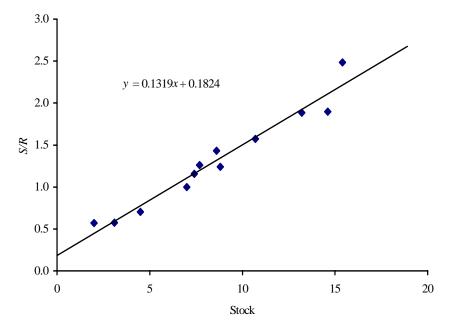


Figure 4. Application of S-R data in the linearized Beverton-Holt S-R relationship.

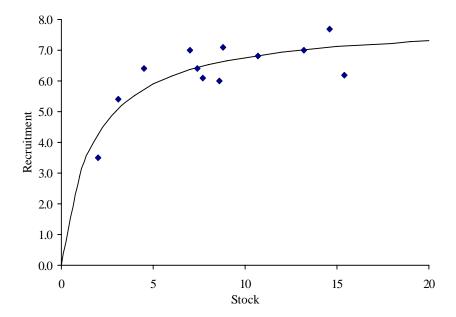


Figure 5. Application of S-R data in the Beveton-Holt S-R relationship.

The general form of the Ricker model is rearranged as follows:

$$R = \alpha S e^{-S\beta}$$

$$R/S = \alpha e^{-S\beta}$$

$$\ln(R/S) = \ln \alpha - \beta S.$$

In the rearranged form, the Ricker *S-R* relationship conforms to the basic linear model:

$$y = ax + b$$

where
$$y = \ln(R/S)$$

 $a = \text{slope} = \beta$
 $x = S$
 $b = \text{intercept} = \ln \alpha$.

The α and β parameters are estimated by regressing $\ln(R/S)$ against S. After taking the anti- $\ln \alpha$, these values are then used to plot a predicted Ricker S-R curve, or can be used as starting values for non-linear regression methods.

Example 2: Utilizing the same data as in Example 1, use the Ricker model to solve for α and β performing both linear and non-linear regression.

The data are fit to a linear model using a regression of $\ln(R/S)$ versus S (Figure 6). The value of α is equal to the inverse ln of the y-intercept, therefore $\alpha = e^{0.7427} = 2.1016$. The value of β is equal to the negative slope, therefore, $\beta = 0.1071$. Non-linear regression is performed using **Solver** in *Excel* and the linear regression parameter values as

starting values. The new parameter values are $\alpha = 1.9704$ and $\beta = 0.1015$. The Ricker model is graphed onto the original data using the non-linear regression parameter values (Figure 7).

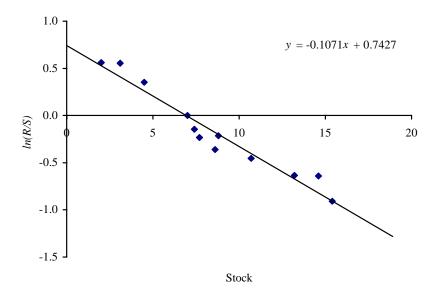


Figure 6. Application of S-R data in the linearized Ricker S-R relationship.

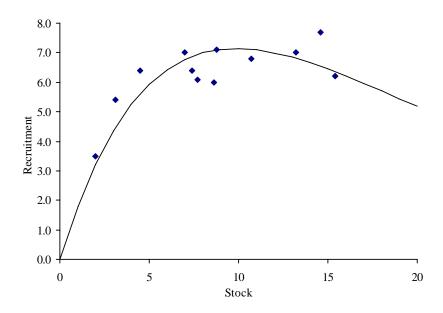


Figure 7. Application of S-R data in the Ricker S-R relationship.

The general form of the Shepherd model is:

$$R = \alpha S / \left[1 + \left(S / K \right)^{\beta} \right] .$$

Shepherd suggest values for β of slightly less than 1 for pelagic fish, about 1 for flatfish, and greater than 1 for those species which cannibalism is believed to be significant. The value of a is estimated by drawing a straight-line through the origin and determining the slope of that line. The parameter K is estimated by choosing "typical" current values of stock and recruitment through which the curve should pass, then estimating values of K from the following:

$$K = \frac{S * / [(\alpha S * / R *) - 1]^{1/\beta}}{[(\alpha S * / R *) - 1]^{1/\beta}}$$
.

Spawning Stock-Per-Recruit and Steady State

The reciprocal of recruits per unit spawning stock is spawning stock per recruit (SSBPR). Recall that this is the corollary output of the yield per recruit model when considering the effects of exploitation. The SSBPR is a measure of survival in the population at various levels of exploitation (*F*). The intersection of these straight-line functions representing various levels of fishing mortality with the *S-R* curve represent equilibrium points (Figure 8).

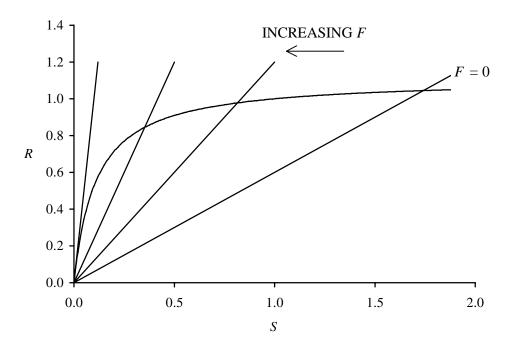


Figure 8. Intersection of SSBPR functions at various fishing mortality levels (F), with a Beverton-Holt S-R relationship.

At the highest level of fishing mortality, there is no intersection with the *S-R* curve, leading to stock collapses.

Exploited Population Trajectories

The two-stage life history trajectory for an exploited population can be described on a S-R / SSBPR plot (Figure 9) where the relationship between the recruit stage and spawning stock stage is described by the straight line with a slope dependent on the level of F, and the S-R curve. At a fixed exploitation rate the stock will return to that intersection point.

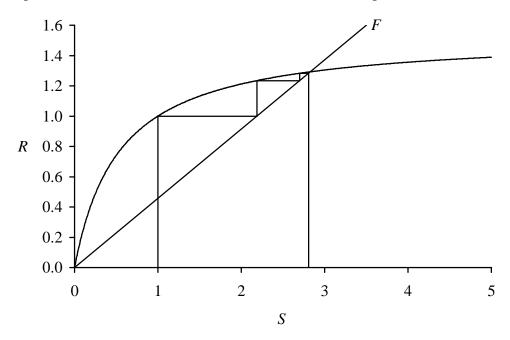


Figure 9. Two-stage life history trajectory based on the intersection of *S-R* and SSBPR relationships.

Environmental Effects on the S-R Relationship with Exploitation

Environmental factors can modify the *S-R* relationship markedly reducing the level of recruitment available for any stock level. However, if the effects of exploitation are superimposed on the *S-R* relationship, the disastrous effects of negative environmental factors and high fishing mortality are evident with the lack of stable equilibrium points (Figure 10). Note that at high levels of fishing mortality and low stock levels, there is no intersection between the unfavorable environment *S-R* curve, and the high fishing mortality curve, leading to stock collapse.

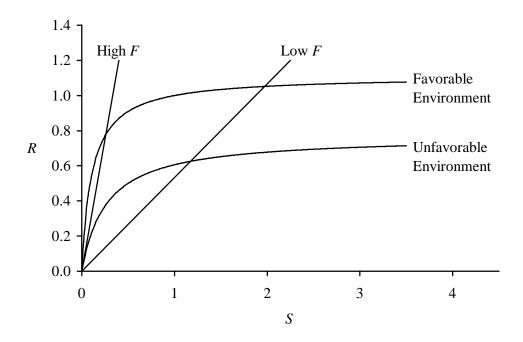


Figure 10. Effect of environmental suitability on the S-R and SSBPR relationships.

Exercises

- 1. Given the following stock-recruitment data, for each species:
 - (a) Plot the time history of spawning stock size and recruitment.
 - (b) Estimate the parameters of a Beverton-Holt stock-recruitment model using both the linear and non-linear regression methods.
 - (c) Estimate the parameters of a Ricker stock-recruitment model using both the linear and non-linear regression methods.
 - (d) Describe and interpret the models for each species over their time history.

	Sh	ad	Salı	non
Year	S	R	S	R
1921			150	449
1922			40	228
1923			70	199
1924			106	81
1925			162	161
1926			253	146
1927			87	162
1928			109	263
1929			90	159
1930			109	117
1931			87	258
1932			74	254
1933			97	219
1934			145	126
1935			88	125
1936			137	135
1937			126	133
1938			123	159
1939			71	183
1940	212	193	88	86
1941	284	188	93	57
1942	237	156	63	69
1943	229	135	92	150
1944	200	113	77	114
1945	123	83	66	126
1946	101	103	44	82
1947	75	129	48	77
1948	86	114	75	81
1949	75	97		
1950	65	80		
1951	89	85		
1952	120	128		
1953	74	163		
1954	77	166		
1955	59	169		
1956	138	157		

	Yellowtai	l Flounder	Blue	Crab
year	S	R	S	R
1956			1.6	2.8
1957			0.5	4.8
1958			0.2	0.3
1959			0	4
1960			0.3	0.5
1961			0.1	0
1962			0.2	1
1963			0.5	0.4
1964			0.2	8.6
1965			0.4	3.7
1966			0.8	3.1
1967			1.6	0.5
1968			3	15.2
1969			1.5	1.5
1970			4.7	17.8
1971			3	7.1
1972			2.1	7.5
1973			0.1	4
1974			0.1	0.7
1975			0	0.7
1976	25.5	50.3	0.1	5.7
1977	18.0	57.1	0.2	6.3
1978	11.9	20.1	0.2	6.4
1979	13.5	14.1	0.4	0.7
1980	9.2	50.5	0.4	12.3
1981	6.7	26.8	0.6	9.3
1982	11.6	23.8	0.6	5
1983	12.9	56.2	0.4	10.5
1984	12.4	20.4	0.3	4.5
1985	16.4	7.4	0.2	8.7
1986	11.4	9.4	0.6	8.5
1987	3.3	17.3	0.4	12.7
1988	2.7	6.3	3.8	17.1
1989	3.8	6.2	4.5	24.3
1990	2.6	17.2	7.1	11.3
1991	2.2	6.6	4	16.8

1957	151	123	
1958	149	119	
1959	154	133	
1960	149	129	
1962	84	105	
1963	101	112	
1964	130	138	
1965	121	144	
1966	133	109	
1967	110	111	
1968	115	128	
1969	160	168	
1970	160	227	

1992	5.1	6.2	1.5	16.2
1993	4.3	16.8	1.2	19.4
1994	3.5	4.9	0.5	12.5
1995	3.7	5.2		

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Chapter IX

BIOMASS DYNAMIC MODELS

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Introduction

A surplus production model was proposed by Schaefer in 1954 and 1957 to describe the relationship between the catch of yellowfin tuna in the eastern tropical Pacific (ETP) and effort. It was based on the assumption that for each level of fishing effort, there was an equilibrium sustainable catch that was equivalent to the surplus production at that particular stock biomass level. If the level of fishing effort changed, the stock biomass was assumed to adjust immediately, and produce a surplus production that would be removed as catch. The basic dome-shaped model used to describe the relationship between surplus production and stock biomass, and catch and effort is conceptually simple. It describes the biological and fishery processes evolving from the logistic model of population growth. Unfortunately, the equilibrium assumption is always violated, therefore, equilibrium models usually result in overly optimistic estimates of $B_{\rm MSY}$.

Model Formulation

The Graham-Schaefer model in the form of a differential equation also can be used to describe the dynamic behavior of stock biomass in non-equilibrium:

$$\frac{dB}{dt} = rB\left(1 - \frac{B}{K}\right) - C$$

where B is stock biomass.

C is catch rate,

r is the intrinsic rate of stock growth, and

K is the unfished stock size at carrying capacity.

The catch rate (*C*) is assumed to be proportional to stock size:

$$C = FB = qfB$$

where C is catch rate,

F is fishing mortality,

q is catchability coefficient, and

f is fishing effort.

Rearranging this equation:

$$CPUE = \frac{C}{f} = qB$$
.

The catch per unit effort (C/f or CPUE) is directly proportional to stock abundance, through q, the catchability coefficient. This equation describes an "observation model" that may result from a fishery or survey CPUE.

In the discrete-time form the previous differential equation describing the stock biomass time series can be rewritten (Walters and Hilborn 1976):

$$B_{t+1} = B_t + rB_t \left(1 - \frac{B_t}{K} \right) - C_t$$

where B_{t+1} is the stock biomass in year t+1,

 B_t is the stock biomass in year t,

K is the unfished stock biomass at carrying capacity, and *r* is the intrinsic rate of stock growth.

The Graham-Schaefer model is symmetrical, and therefore surplus production is maximized at ½

K. The term $\left(1 - \frac{B_t}{K}\right)$ provides density dependent feedback into the model, and thus

modulates stock growth at high stock biomass. As B_t approaches K (high biomass), the term approaches 0, and stock growth is zero. As B_t approaches 0 (low biomass), the term approaches 1, and stock growth is maximum. Catch rates in excess of stock biomass surplus production result in stock decline. Conversely, catch rates less than stock biomass surplus production result in stock expansion.

Example 1: Use the discrete form of the dynamic biomass equation to investigate the sensitivity of the model output, B_t , to variations in catch, and in the input parameters B_0 , K, and r.

(A) Evaluate the effect of the intrinsic rate (r) on stock biomass and growth rate assuming a starting biomass (B_0) of 1 mt and a carrying capacity (K) of 100 mt, and zero catch. Note that limits on r for most marine fishery resources are: 0.1 < r < 1, therefore evaluate r values of 0.2, 0.4, 0.6, and 0.8.

The biomass at a function of time is described by:

$$B_{t+1} = B_t + (r) \left(B_t \sqrt{1 - \left(\frac{B_t}{K} \right)} \right) - C_t$$

(A1) Effect of the intrinsic rate of growth (r) on the stock biomass trajectory (B_t) .

Results: B_t

Figure 1. Effect of the intrinsic rate of growth (r) on the stock biomass trajectory (B_A) .

Conclusion: Increasing r increases the rate of stock biomass growth, thus decreasing the time required for B_t to approach K.

(A2) Effect of the intrinsic rate of growth (r) on $\frac{dB}{dt}$ the stock biomass trajectory (B_t).

Results: B_t

Figure 2. Effect of the intrinsic rate of growth (r) on the stock biomass growth rate $\binom{dB}{dt}$ as a function of biomass (B).

Conclusion: Increasing r increases the maximum rate of growth. Note that maximum production occurs at stock biomass levels of $\frac{K}{2}$.

- (B) Evaluate the effect of catch on the stock biomass trajectory using a variety of catch histories, B_0 , at 25, 50, and 100 mt, r = 0.5, and K = 100 mt.
- (B1) Constant catch of 10 mt.

Results:

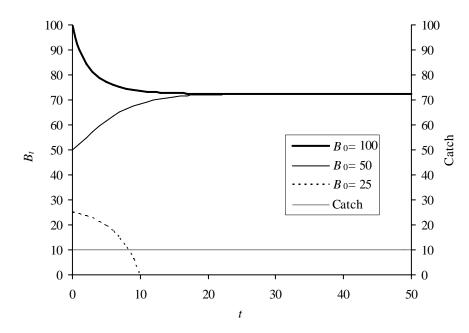


Figure 3. Effect of a constant catch of 10 mt on the stock biomass trajectory.

Conclusions: The annual catch of 10 mt is 10% of K, and after approximately 20 years, the stock biomass asymptotes in quasi-equilibrium at a level of 72 mt for the B_0 of 100 and 50 mt. However, if B_0 is 25 mt, then the stock collapses after 10 years. In other words, with r = 0.5, the stock could not support a constant catch of 40% of B_0 .

(B2) Increasing catch from 0 to 50 mt over a 50 year period.



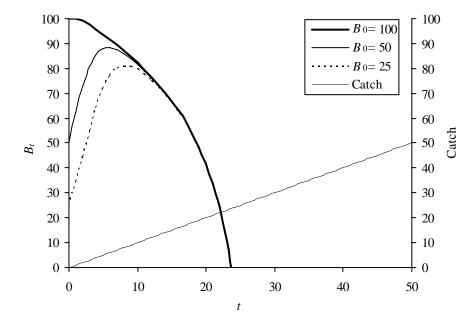


Figure 4. Effect of increasing catch from 0 to 50 mt on the stock biomass trajectory.

Conclusions: At low catch levels, between 0-5 mt, stock biomass increased. However, as catch increased beyond 5 mt, stock biomass steadily declined, reaching 0 mt at 23 years at a catch level of about 20 mt.

(B3) Oscillating catch with a 10 year period, and maximum value of 15 mt.

Results:

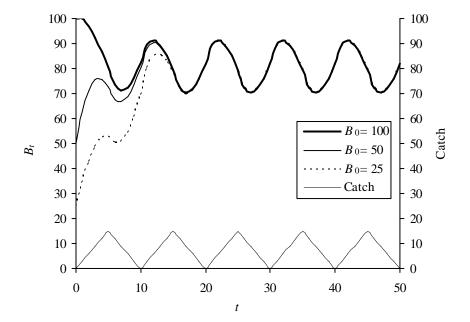


Figure 5. Effect of an oscillating catch with a period of 10 years and maximum of 15 mt on the stock biomass trajectory.

Conclusions: Within the specified range of initial stock biomass levels, mean stock biomass stabilizes at 80 mt with an oscillation \pm 10 mt, almost 180° out of phase with the oscillating catch after 12 years, that is periods of low stock biomass levels follow periods of high catch by about 3 years.

(B4) Oscillating catch with a 10 year period, and a maximum value of 25 mt.

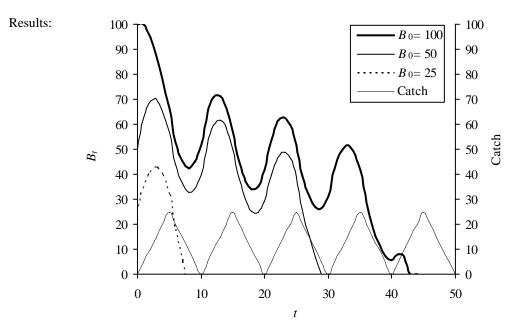


Figure 6. Effect of an oscillating catch with a period of 10 years and a maximum of 25 mt on the stock biomass trajectory.

Conclusions: Within the specified range of initial stock biomass levels, the stock declines to 0 mt biomass. At the lowest initial stock biomass level (25 mt), stock collapse occurs in 8 years, and at 50 and 100 mt initial stock biomass levels, stock collapse occurs in 29 and 43 years, respectively. Thus, when r = 0.5, the stock can not support maximum catch of 25 mt.

Other management parameters that result from the surplus production models are:

Fishing Rate at MSY
$$(F_{MSY}) = \frac{r}{2}$$

Effort at $F_{MSY}(f_{MSY}) = \frac{F_{MSY}}{q} = \frac{r}{2q}$
Maximum Sustainable Yield (MSY) = $\frac{rK}{4}$
Stock Biomass at MSY $(B_{MSY}) = \frac{K}{2}$

Parameters of the model (B_A, r, K) are estimated assuming measurement error in the observation model in the form of a time series. The input data are catch history and a historical index of relative abundance for observational model.

The output of the retrospective model is a time-series of estimated past stock biomass levels, and an estimated index of relative abundance. The parameters of the model are estimated through a minimization of the sum of the squares of the residuals between the observed and estimated indices of relative abundance. The estimated index of relative abundance is determined by

multiplying the estimated biomass by the mean catchability coefficient (q). The catchability coefficient at each time step is estimated by dividing the observed index of abundance by the estimated mean biomass at that time-step. Thus the parameters that are estimated in the model are r, K, B_t , and q, and initial values for each parameter must be guessed to start the estimation process.

Example 2: Consider the following 50 year time series of catch and survey index. Determine an estimated survey index, r, K, and B_0 , and the relevant fishery management parameters (MSY and B_{MSY}).

Year	Catch (mt)	Observed Survey Index
1950	0	0.0050
1951	5	0.0063
1952	10	0.0069
1953	15	0.0070
1954	20	0.0065
1955	15	0.0057
1956	10	0.0054
1957	5	0.0056
1958	0	0.0064
1959	5	0.0075
1960	10	0.0080
1961	15	0.0078
1962	20	0.0071
1963	15	0.0062
1964	10	0.0058
1965	5	0.0061
1966	0	0.0067
1967	5	0.0078
1968	10	0.0082
1969	15	0.0079
1970	20	0.0073
1971	15	0.0062
1972	10	0.0059
1973	5	0.0061
1974	0	0.0068
1975	1	0.0079
1976	2	0.0086
1977	3	0.0090
1978	4	0.0092
1979	5	0.0091
1980	6	0.0090
1981	7	0.0089
1982	8	0.0087
1983	9	0.0084
1984	10	0.0082
1985	11	0.0079
1986	12	0.0077
1987	13	0.0074
1988	14	0.0070
1989	15	0.0067
1990	16	0.0063
1991	17	0.0059
1992	18	0.0054
1993	19	0.0048

1994	20	0.0042
1995	21	0.0034
1996	22	0.0024
1997	10	0.0011
1998	5	0.0006
1999	1	0.0004

Methods: To fit the discrete time model, a time series of biomass and an index of relative abundance must be estimated. Initial values of the model parameters must be selected. The stock intrinsic rate of growth should be greater than 0.1, and less than 1 for most marine fishery resources, so 0.5 is a reasonable initial value. The carrying capacity (K) of the environment for the stock could be from 2 to 20 times greater than the annual catch, depending on the magnitude of the fishery relative to the status of the stock. For highly-fecund, short-lived species (relatively high r), K could be 5-7 times greater than sustainable annual catch. For longer-lived species, with relatively less reproductive potential (mid range r), K could be 8-15 times greater than a sustainable annual catch. Finally, an initial biomass (B_0) must be selected. A reasonable starting value is 50% of the initial carrying capacity K.

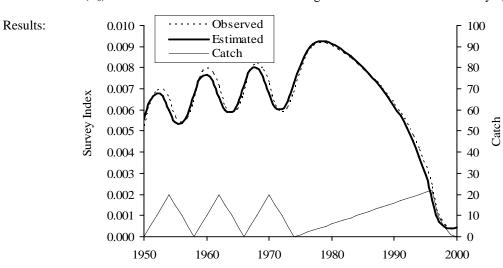


Figure 7. Time-series plot of catch and observed and estimated indices of relative abundance.

Estimated fishery parameters are:

$$r = 0.444$$

 $K = 107.94$ mt
 $B_{MSY} = \frac{K}{2} = 54.4$ mt
 $MSY = \frac{rK}{4} = 11.9$ mt

Conclusions: The observed survey index time series was based on a deterministically generated biomass time series estimated with the following input parameters: K = 100 mt, $B_0 = 50$ mt, r = 0.5. Additionally, the observed survey index was based on the biomass at the start of the year. The estimated and observed indices of relative abundance track reasonably well, as a result of the contrast in the observed index (Hilborn and Walters 1992), and the difference is due to the fact that the estimated survey index is based on a mid-year biomass, whereas the observed survey index is based on a start of the year biomass. As a result, the dynamic biomass model overestimated K by 8% and underestimated K by 11%. The estimated K are 54.4 and 11.9 mt, respectively. The actual K are 50 and 12.5 mt, respectively. Thus, the model overestimated K by 8% and underestimated K by 5%. This is because the data were generated based on K at the start of the year, whereas the model is fit using an mid year K1.

Example 3: Consider the following data for yellowfin tuna from the eastern tropical Pacific (ETP) from Schaefer 1957. Determine an estimated CPUE, r, K, and B_0 , and the relevant fishery management parameters (MSY, B_{MSY} , and f_{MSY}). Catch is in units of 1000s of pounds and effort is in units of standardized class 4 clipper days.

Year	Catch	Effort
1934	60913	5879
1935	72294	6295
1936	78353	6771
1937	91522	8233
1938	78288	6830
1939	110417	10488
1940	114590	10801
1941	76841	9584
1942	41965	5961
1943	50058	5930
1944	64094	6397
1945	89194	9377
1946	129701	13958
1947	160134	20381
1948	200340	23984
1949	192458	23013
1950	225810	31856
1951	183685	18726
1952	192234	31529
1953	138918	36423
1954	138623	24995
1955	140581	17806

Methods: Use the catch (C) and effort (f) data to generate an index of relative abundance, CPUE = C/f, then fit the model as before.

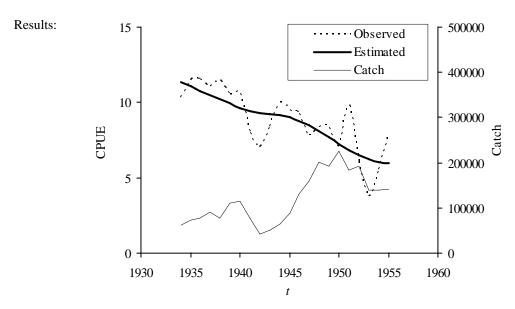


Figure 8. Time-series plot of catch and observed and estimated CPUE.

The estimated stock biomass fishery parameters are:

$$r = 0.0798$$

 $K = 3,698,675$
 $q = 0.0000027$
 $B_{MSY} = \frac{K}{2} = 1,849,338$
 $MSY = \frac{rK}{4} = 73,768$
 $f_{MSY} = \frac{r}{2q} = 14,658$

Conclusion: The Schaefer equilibrium surplus production model estimated an MSY of approximately 190,000 units (1000s of pounds) at an $f_{\rm MSY}$ of 32,000 units (class 4 clipper days) (Schaefer 1957). Note that non-equilibrium dynamic biomass model results in more conservative values of MSY and $f_{\rm MSY}$ compared to the equilibrium model, that is the equilibrium model overestimates both MSY and $f_{\rm MSY}$ by more than 200%.

Exercises

- 1. (a) Determine the surplus production curve dB/dt for $B_t = 0$ to 100 mt, with K = 100 mt and r = 0.5. Based on interpolation of results from Example 1A, the maximum surplus production should be about 12.5 mt occurring at $B_t = 50$ mt. Note that the dome-shaped model that describes surplus production indicates that there are two quasi-equilibrium biomass levels that can sustain any constant catch level below the maximum sustainable yield.
 - (b) Using the discrete time model over a period of 50 years, and for B_0 and K = 100 mt and r = 0.5, vary catch levels intermittently to drive the stock biomass to the two levels that would sustain a constant catch of 8 mt for at least 10 years. Illustrate the result as a time-series indicating B_t and C_t over the 50 year period. This demonstrates that in the quasi-equilibrium condition, the Schaefer model is conceptually sound.
- 2. Consider the following data for the mid-Atlantic bluefish stock for the period 1974-1997.

Year	Catch	Inshore Survey - Fall Index	Recreational Fishery CPUE
74	34004	1.484	
75	31179	5.587	
76	30384	5.724	
77	30785	6.546	
78	30566	5.875	
79	45776	7.443	4.797
80	48845	7.031	4.765
81	51401	13.284	7.332
82	43005	4.823	5.741
83	48383	3.958	4.117
84	36607	7.682	4.604
85	30444	3.451	3.321
86	50106	3.913	4.844
87	41540	2.703	4.518
88	30068	1.982	2.435
89	23439	9.132	1.688
90	21035	2.513	1.391
91	22350	2.063	1.251
92	17187	1.363	1.138
93	14655	0.736	0.961
94	12153	1.673	0.826
95	10836	2.054	1.000
96	11348	2.264	1.277
97	11606	1.367	1.226

- (a) Using the fall inshore survey as the index of relative abundance, estimate a stock biomass trajectory and survey index for the period, and the surplus production model parameters K and r. Finally, determine MSY and B_{MSY} .
- (b) Repeat the above analysis, adding a second index of relative abundance. Is the result different? Why?

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Chapter X

AGE AND LENGTH STRUCTURED STOCK ASSESSMENT MODELS

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Background

Age and length structured models (e.g. sequential population analysis, virtual population analysis, statistical catch at age models) utilize catch at age or length to reconstruct the population dynamics of exploited fish stocks, providing estimates of mortality rates and absolute population abundance. These models provide an advantage over stock-production (Schaefer 1954) and dynamic pool (Beverton and Holt 1957) models in that they specifically track the abundance of individual cohorts of fish over time. More traditional models require data on effort, catchability or gear selectivity.

Megrey (1989) provides a comprehensive review and comparison of age-structured stock assessment model development from both theoretical and applied points of view. Baranov (1918) was the first fisheries scientist to propose the approach of using data describing the mean age structure of the catch across multiple years to calculate the contribution of each cohort in the stock to each year's total catch (Megrey 1989). Baranov's conceptual approach was that the population size of a cohort at the time the cohort enters the exploitable stock can be approximated by simply summing the catches removed from that cohort during the years it contributes to the fishery. This method considered natural mortality to be negligible as compared to fishing mortality, so the estimated stock size or cohort initial abundance is a minimum estimate, and the estimated rate of exploitation is always greater than the true rate of exploitation.

Fry (1957) further developed Baranov's methodology by analyzing age structure of the population annually; he referred to the minimum population estimate calculated by this method as the "virtual population." He defined the virtual population as "the sum of the fish, belonging to a given year class, present in the water at any given time that are destined to be captured in the fishery in that year and all subsequent years."

Beverton and Holt (1957) provided explicitly for natural mortality in their formulation of an agestructured model. Gulland (1965) combined Baranov's catch equation with Fry's formulation. His procedure was started by providing a guess of the fishing mortality rate for the oldest age in the cohort "the terminal F." Non-linear sequential computations are then made backward in time at one-year intervals to reconstruct cohort abundance. The solutions to these non-linear equations are iterative, and therefore cumbersome. Pope (1972) proposed a less complicated model that greatly simplified the computations needed to calculate a solution to the non-linear sequential model. Pope's model was based on an approximation to the non-linear sequential model in which the curve describing the exponential decrease in population numbers was replaced by a step function. That is, the approximation was that all the fish captured in any age group were taken exactly halfway through the year. With Pope's approximation, population abundance estimates and fishing mortality rates could be calculated directly from catch data without the need for an iterative procedure. Jones (1974) proposed a length-based modification to the Pope (1972) age-based analysis.

A limitation of age-structured models at this point in their development was that cohorts were not linked. Abundance, fishing mortality, and selectivity were estimated annually for each age by analyzing catch at age data one cohort at a time. Parameter values estimated from one cohort were not related to those from other cohorts in the stock. Doubleday (1976) introduced the separability assumption to improve this situation by representing fishing mortality as the product of age-specific selectivity and year-specific exploitation rate .

These "backward projection" age-structured models have evolved considerably in the last several decades. Modifications and enhancements have given rise to a wide range of modeling options. These options go by a variety of names (that are often used interchangeably by different scientists), including virtual population analysis, cohort analysis, sequential population analysis (SPA), and extended survivors analysis. Some of these models include the option to use age-specific indices of relative population abundance to "tune" the model; tuning is a process by which fishing mortality or abundance of fish-at-age in the terminal year of the model is determined by incorporating information from an index (or indices) of abundance. Boot-strapping statistical methods have been added to provide estimates of uncertainty to the basic deterministic equation. One can also utilize existing stock abundance data grouped by age or length and specified fishing mortality rates to project future catches and stock abundances.

All of the age-structured models discussed so far use historical catch at age or length data and an assumed natural mortality rate to backcalculate fishing mortality rates and absolute stock abundance. An alternative approach is the forward projecting statistical catch at age (SCAA) model. As their name implies, SCAA models use catch at age data and one or more indices of abundance to estimate population size and recruitment in the first year of the analysis. The model then reconstructs the population forward from the first to last year by determining what abundance at age, fishing mortality, and selectivity must have been in order to explain the observed catch at age and trends in abundance.

These are called "statistical" models because their parameters (e.g. abundance and fishing mortality) are estimated using a process called maximum likelihood estimation. To obtain the most likely ("maximum likelihood") parameter estimates given the available data, parameter estimates are tweaked until the observed and predicted values for catch at age and abundance index data line up as closely as possible. One major advantage of SCAA over other agestructured analyses (e.g. SPA or VPA) is that SCAA does not assume that catch at age is known without error. Alternative versions of SCAA go by a variety of names including integrated analysis, Stock Synthesis, and ASAP. The latter two names refer to the software used to implement these specific model formulations.

In depth exploration of SPA: Formulation of the Governing Equations for SPA

Projection models predict future cohort abundance and catch based on past cohort abundance and specified levels of fishing and natural mortality based on age or length.

Retrospective models estimate historical levels of abundance and fishing mortality rates from catch data and an assumed natural mortality. These models can be age or length-based.

To develop a quantitative understanding of projection and retrospective models, consider a fish with the following growth and mortality characteristics that are stocked annually into a small pond. These fish have a life span of 5 years, therefore natural mortality is 0.7 or 50% annual loss (Figure 1).

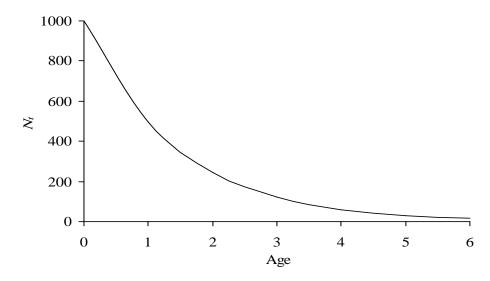


Figure 1. Trajectory of cohort number for a life span of 5 years, where natural mortality is M = 0.7 or 50% annual loss.

The fish also grow rapidly (K = 1.0) to a maximum length of 40 cm, and reach 25 cm at age 1 (Figure 2).

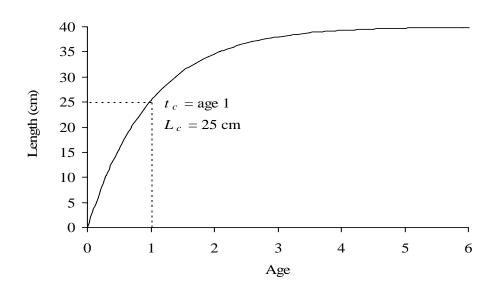


Figure 2. Von Bertalanffy growth function for the pond fish when K=1.0 and $L_{\infty}=40$ cm.

Projection Models: Age-Based

Age-based projection models are based on the exponential decay model and the Baranov catch equation.

The exponential decay model is:

$$N_t = N_0 e^{-(F_t + M)t} = N_0 e^{-Z_t t} = N_{t-1} e^{-(F + M)} = N_{t-1} e^{-Z}$$

where N_0 is the cohort abundance at age 0,

 N_{t-1} is the cohort abundance at age t-1 year,

 N_t is the cohort abundance at age t,

 F_t is the fishing mortality for age t,

M is the natural mortality, and

 Z_t is the total mortality for the age t.

Survival is the proportion of a cohort remaining at each age:

$$S = N_t / N_{t-1} = e^{-Zt} = e^{-(F+M)}$$
.

The Baranov catch equation is:

$$C_{t} = N_{t} \left(\frac{F_{t}}{Z_{t}} \right) \left(1 - e^{-Zt} \right)$$

where C_t is the catch at the age t,

 F_t/Z_t is the proportion dying due to the fishery for the *t*th age, and $(1-e^{-Zt})$ is the mortality rate for the *t*th age.

Catch at age t is also estimated as:

$$C_{t} = \left[N_{t} - N_{t+1}\right]^{F_{t}} Z_{t}.$$

Example 1: Consider a pond stocked with 500 age 1 fish, and that during subsequent years, 75% are lost equally to fishing and natural each year. Project trajectories of catch and cohort number remaining for years 2 to 6.

If 500 fish are stocked, and 75% are lost, then 25% must remain. Therefore, survival (S) is 25% of 500 from the first to second years.

$$S = 0.25 = \frac{N_t}{N_{t-1}} = e^{-Z} = e^{-(F+M)}$$

$$Z = 1.4 = F + M$$

because F = M, therefore F = M = 0.7

Using $N_t = N_{t-1}e^{-(F+M)}$, the trajectory of cohort number is determined (Figure 3 and Table 1). Catch is 50% of the annual loss (Table 1).

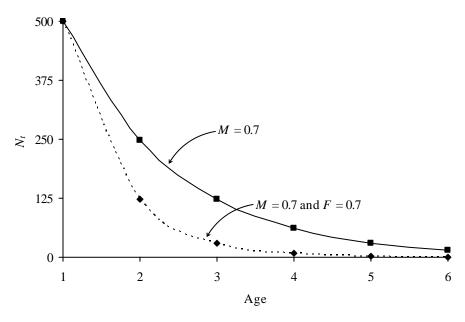


Figure 3. Trajectory of cohort number for F = 0.7 and M = 0.7.

Table 1. Age-based projection of cohort abundance and catch.

Year	Abundance $F = 0.0$	Abundance $F = 0.7$	Catch
1	500	500	188
2	248	123	46
3	123	30	11
4	61	7	3
5	30	2	1
6	15	0.5	
		Total Catch	250

Projection Models: Length-Based

Length-based projection models estimate cohort abundance at specified lengths, and these lengths are determined using the von Bertalanffy growth function.

The exponential decay equation:

$$N_{t} = N_{0}e^{-Zt} = N_{0}e^{-(F_{t}+M)t}$$

is combined with the simplified von Bertalanffy growth equation:

$$L_t = L_{\infty} \left(1 - e^{-Kt} \right)$$

where L_t is the length at age t,

 L_{∞} is the maximum length, and

K is the growth coefficient.

This results in:

$$N_{\scriptscriptstyle t} = N_{\scriptscriptstyle 0} e^{-z \left[-\left(\frac{1}{K}\right) \ln\left(1 - \frac{L_{\scriptscriptstyle t}}{L_{\scriptscriptstyle \infty}}\right)\right]}$$

because the simplified von Bertalanffy equation can be rearranged and solved for t:

$$\begin{split} & \frac{L_t}{L_{\infty}} = \left(1 - e^{-Kt}\right) \\ & \left(\frac{L_t}{L_{\infty}} - 1\right) = -e^{-Kt} \\ & - \ln\left(\frac{L_t}{L_{\infty}} - 1\right) = -Kt \\ & - \frac{1}{K}\ln\left(1 - \frac{L_t}{L_{\infty}}\right) = t \; . \end{split}$$

Example 2:

(A) Reconsider the growth and natural mortality characteristics of the pond fish, and determine the number of fish remaining from a single cohort as a function of length, starting with 1000 age 0 recruits.

$$N_t = N_0 e^{-M\left(-\left(\frac{1}{K}\right)\ln\left(1 - \frac{L_t}{L_{\infty}}\right)\right)}$$

$$N_t = 1000e^{-0.7 \left(-\left(\frac{1}{1.0}\right) \ln\left(1 - \frac{L_t}{40}\right)\right)}$$

Where L_t is 0, 5, 10, 15, 20, 25, 30, 35, and 40 cm.

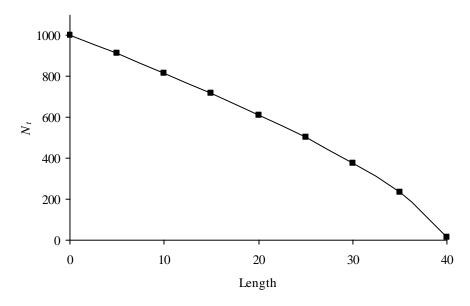


Figure 4. Number of fish remaining in a cohort as a function of the length with natural mortality only.

(B) Now consider the effect of adding an equal amount of fishing mortality to natural mortality (0.7) on all fish larger than 25 cm or age 1. Project the trajectory of cohort number and catch as a function of length for lengths from 25 to 40 cm.

Adding fishing mortality results in a total estimated catch of 256 fish, 0 fish at a length of 40 cm (Figure 5 and Table 2).

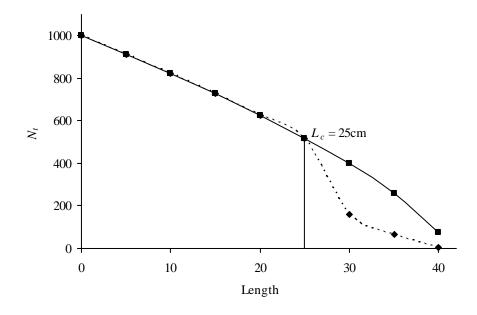


Figure 5. Number of fish remaining in cohort number as a function of length.

Table 2. Length-based projection of cohort abundance and catch.

Length	Abundance $F = 0.0$	Abundance $F = 0.7$	Catch
0	1000	1000	
5	913	913	
10	822	822	
15	727	727	
20	626	626	
25	518	518	
30	398	159	180
35	260	68	45
40	74	6	31
		Total Catch	256

Retrospective Models: Age-Based

Age-based retrospective models either assume natural and fishing mortality act simultaneously during the year, and that the catch is derived continuously during the year (virtual population analysis) or assume only natural mortality acts during the entire year, and that catch is taken instantly mid-way through the year (cohort analysis).

In virtual population analysis, the catch equation is rearranged to estimate the abundance of the cohort at oldest age:

$$N_{t} = \frac{C_{t}Z_{t}}{F_{t}(1 - e^{-Zt})}$$

$$N_{t} = \frac{C_{t}(F_{t} + M)}{F_{t}(1 - e^{-(F_{t} + M)})} *.$$

The fishing mortality rate for the tth age is estimated using the catch from the tth age, cohort abundance from the previous older age (N_{t+1}) and an assumed natural mortality. The exponential decay equation is rearranged to estimate cohort abundance at younger ages, and is also substituted into a rearranged catch equation:

$$N_{t} = \frac{N_{t+1}}{e^{-Zt}}$$

$$\frac{N_{t+1}}{e^{-Zt}} = \frac{C_{t}Z_{t}}{F_{t}(1 - e^{-Zt})}.$$

The equation is rearranged and expanded with unknown F_t s on one side of the equation for iterative solving:

$$N_{t+1} / C_t = \frac{[(F_t + M)]e^{-(F_t + M)}}{F_t (1 - e^{-(F_t + M)})}$$
 *

The starred (*) equations are alternatively and repetitively solved to develop a history of cohort abundance and fishing mortality rates.

Cohort analysis is a simplification of virtual population analysis where it is assumed that the catch is taken instantly in the middle of the year (t + 0.5), and that natural mortality occurs equally during the first and second halves of the year.

Figure 6 describes the trajectory of cohort numbers during a single year.

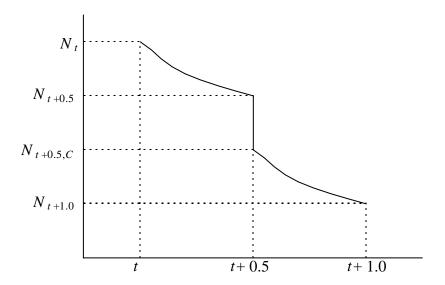


Figure 6. Cohort number as a function of time, during one year, showing the Pope's age-based approximation with catch taken instantaneously at mid-year.

In Figure 6:

 N_t is the number of fish in the cohort at age t at the beginning of the year,

 $N_{t+0.5}$ is the number of fish in the cohort at age t halfway through the year, before fishing, and is expressed as:

$$N_{t+0.5} = N_t e^{-M/2}$$
,

 $N_{t+0.5,C}$ is the number of fish in the cohort at age t, halfway through the year, after fishing, including catch, and is expressed as:

$$N_{t+0.5,C} = N_t e^{-M/2} - C_t$$

 $N_{t+1.0}$ is the number of fish in the cohort at age t+1, and is expressed as:

$$N_{t+1.0} = \left[N_t e^{-M/2} - C_t \right] e^{-M/2}.$$

As before, the catch equation is rearranged to estimate the abundance of the cohort at the oldest age:

$$N_{t} = \frac{C_{t}(F_{t} + M)}{F_{t}(1 - e^{-(F_{t} + M)})}$$
.*

The number of fish in the cohort at the *t*th age is estimated from the number available at the older age (t+1), catch at the *t*th age, and natural mortality. The equation describing the number of survivors at the end of the year (N_{t+1}) is rearranged to provide:

$$N_{t} = \left[\left(N_{t+1} \right) \left(e^{\frac{M}{2}} \right) + C_{t} \right] e^{\frac{M}{2}} .*$$

The fishing mortality rate at the *t*th age is estimated by rearranging the exponential decay equation as follows:

$$N_{t+1} = N_t e^{-Z_t}$$

$$Z_{t} = -\ln\left(\frac{N_{t+1}}{N_{t}}\right) = F_{t} + M$$

$$F_{t} = -\ln \left(\frac{N_{t+1}}{N_{t}} \right) - M \quad .*$$

The starred (*) equations are alternatively and repetitively solved to develop a history of cohort abundance and fishing mortality rates.

Both virtual population analysis and age-based cohort analysis require catch at age data to estimate cohort abundance at age and fishing mortality rates at age. Abundance and fishing mortality rates for a single cohort or year-class over a period of years or ages can be represented as single columns, and are the outputs from the sequential population analysis of a column of input catch at age data.

Consider the form of the following columns of input and output data for a single cohort of fish where $C_{x,y,z}$, $N_{x,y,z}$, and $F_{x,y,z}$ represent catch, abundance, and fishing mortality of the xth age during the yth year and of the zth year class or cohort.

Single Cohort - 1990

Input	Ou	tput
$C_{0,90,90}$	$N_{0,90,90}$	$F_{0,90,90}$
$C_{1,91,90}$	$N_{1,91,90}$	$F_{1,91,90}$
$C_{2,92,90}$	$N_{2,92,90}$	$F_{2,92,90}$
$C_{3,93,90}$	$N_{3,93,90}$	$F_{3,93,90}$
$C_{4,94,90}$	$N_{4,94,90}$	$F_{4,94,90}$
$C_{5,95,90}$	$N_{5,95,90}$	$F_{5,95,90}$
$C_{6,96,90}$	$N_{6,96,90}$	$F_{6,96,90}$

Example 3: Given the following age-based catch history for this cohort (year class), ages (0-5), and an assumed natural mortality of 0.7 based on maximum age of an individual in the cohort and life history characteristics of the species, estimate how many fish were initially recruited to the cohort, the cohort abundance trajectory over the life span and the level of fishing mortality each year.

Age	Catch
5	1
4	3
3	12
2	47
1	188
0	0

Total Catch:

251 fish over the life span of the cohort.

Solution Using Virtual Population Analysis:

Step (1) Using the catch at age 5, the assumed natural mortality rate (*M*) of 0.7, and an assumed fishing mortality (*F*) at age 5 of 0.7, a rearranged Baranov catch equation is used to solve for abundance of fish at age 5.

$$N_{5} = \frac{C_{5}(Z_{5})}{F_{5}(1 - e^{-Z_{5}})} = \frac{C_{5}(F_{5} + M)}{F_{5}(1 - e^{-(F_{5} + M)})}$$

$$N_{5} = \frac{1(1.4)}{0.7(1 - e^{-1.4})}$$

$$N_{5} = \frac{1.4}{0.7(1 - 0.25)} = \frac{1.4}{0.5} = 3$$

Step (2) The fishing mortality rate at age 4 fish is estimated by iteratively solving the combined exponential decay and catch equation.

$$N_5 / C_4 = 3/3 = (F_4 + M)e^{-(F_4 + M)} / F_4 (1 - e^{-(F_4 + M)})$$

where M = 0.7, and iteratively solving for F_4

$$F_4 = 0.56$$

Step (3) The abundance of age 4 fish is next estimated using the rearranged catch equation.

$$N_4 = {C_4 Z_4 \over F_4 \left(1 - e^{-Z_4} \right)} = {C_4 \left(F_4 + M \right) \over F_4 \left(1 - e^{-\left(F_4 + M \right)} \right)}$$

$$N_4 = 3 (0.56 + 0.7) / \\ 0.56 (1 - e^{-(0.56 + 0.7)})$$

$$N_4 = \frac{3(1.26)}{0.56(1-0.28)} = \frac{3.78}{0.40} = 9$$

- Step (4) The fishing mortality rate at age 3 fish is estimated as in Step (2).
- Step (5) The abundance of age 3 fish is estimated as in Step (3).

and so on.

Results of Virtual Population Analysis:

Age	Catch	Estimated N	Actual N	Estimated F	Actual F
0	0	1049	1000	0.00	0.00
1	188	521	491	0.66	0.70
2	47	134	122	0.64	0.70
3	12	35	30	0.62	0.70
4	3	9	7	0.56	0.70
5	1	3	2	0.70	0.70

Conclusion: The estimated initial N is 1049 compared to the actual N of 1000, and the estimated F values of 0.66, 0.64, 0.63, 0.56, and 0.70 on the exploited ages compared to the actual F values of 0.7.

Solution Using Cohort Analysis:

Step (1) Using the catch at age 5, the assumed natural mortality rate (M) of 0.7, and an assumed fishing mortality rate (F) at age 5 of 0.7, a rearranged Baranov catch equation is used to estimate the abundance of fish at age 5.

$$N_5 = C_5 / [F_5 / (F_5 + M)] [1 - e^{-(F_5 + M)}]$$

$$N_5 = \sqrt{\left[0.7/(0.7 + 0.7)\right]} \left[1 - e^{-(0.7 + 0.7)}\right]$$

$$N_5 = 1/(0.7/1.4)(1-0.25)$$

$$N_5 = \frac{1}{(0.5)(0.753)} = \frac{1}{0.375} = 2.65$$

Step (2) The abundance of age 4 fish is then estimated for using Pope's cohort analysis method, and the abundance at age 5 (estimated above in Step 1), catch at age 4, and the assumed natural mortality.

$$N_4 = \left[\left(N_5 \right) \left(e^{\frac{M_2}{2}} \right) + C_4 \right] e^{\frac{M_2}{2}}$$

$$N_4 = \left[(2.65) \left(e^{0.7/2} \right) + 3 \right] e^{0.7/2}$$

$$N_4 = (3.76 + 3)1.42 = 9.60$$

Step (3) Fishing mortality of age 4 fish is estimated by comparing the abundance of age 5 fish to age 4 fish, allowing for natural mortality.

$$F_4 = \ln \left(\frac{N_4}{N_5} \right) - M$$

$$F_4 = \ln\left(\frac{9.60}{2.65}\right) - 0.7 = 1.29 - 0.7 = 0.59$$

- Step (4) Abundance of age 3 fish is estimated as in Step (2).
- Step (5) Fishing mortality of age 3 is estimated as in Step (3).

and so on.

Results of Age-Based Cohort Analysis:

Age	Catch	Estimated N	Actual N	Estimated F	Actual F
5	1	3	2	0.70	0.70
4	3	10	8	0.59	0.70
3	12	36	31	0.63	0.70
2	47	140	125	0.65	0.70
1	188	549	500	0.67	0.70
0	0	1105	1000	0.00	0.00

Conclusion:

The estimated initial N is 1105 compared to the actual N of 1000; and the estimated F values of 0.70, 0.59, 0.63, 0.65, and 0.67 on the exploited age classes compared reasonably well to the actual F values of 0.70.

The form of the complete matrix of input catch at age data for a stock of a relatively short-lived animal is as follows:

Harvest	Catch at Age					Total	
Year	0	1	2	3	4	5	Catch
1990	$C_{0,90,90}$	$C_{1,90,89}$	$C_{2,90,88}$	$C_{3,90,87}$	$C_{4,90,86}$	$C_{5,90,85}$	TC_{90}
1991	$C_{0,91,91}$	$C_{1,91,90}$	$C_{2,91,89}$	$C_{3,91,88}$	$C_{4,91,87}$	$C_{5,91,86}$	TC_{91}
1992	$C_{0,92,92}$	$C_{1,92,91}$	$C_{2,92,90}$	$C_{3,92,89}$	$C_{4,92,88}$	$C_{5,92,87}$	TC_{92}
1993	$C_{0,93,93}$	$C_{1,93,92}$	$C_{2,93,91}$	$C_{3,93,90}$	$C_{4,93,89}$	$C_{5,93,88}$	TC_{93}
1994	$C_{0,94,94}$	$C_{1,94,93}$	$C_{2,94,92}$	$C_{3,94,91}$	$C_{4,94,90}$	$C_{5,94,89}$	TC_{94}
1995	$C_{0,95,95}$	$C_{1,95,94}$	$C_{2,95,93}$	$C_{3,95,92}$	$C_{4,95,91}$	$C_{5,95,90}$	TC_{95}
1996	$C_{0,96,96}$	$C_{1,96,95}$	$C_{2,96,94}$	$C_{3,96,93}$	$C_{4,96,92}$	$C_{5,96,91}$	TC_{96}

where $C_{x,y,z}$ is the catch of the *x*th age during the *y*th year, and the *z*th year-class or cohort. Note that a row in this matrix represents the harvest or catch in a given year (*y*) by age (*x*); a column in this matrix represents the catch for a specific age group (*x*) by year of harvest (*y*); and a diagonal in the matrix represents the catch of a cohort or year-class (*z*) in succeeding years of harvest (*y*) and age (*x*).

The catch data from a single cohort or year-class over a period of years and ages can also be represented as a single column.

Applying sequential population analysis to the previous input catch at age matrix results in output matrices of abundance at age and fishing mortality at age:

Harvest	Abundance at Age						Total
Year	0	1	2	3	4	5	Stock Abundance
1990	$N_{0,90,90}$	$N_{1,90,89}$	$N_{2,90,88}$	$N_{3,90,87}$	$N_{4,90,86}$	$N_{5,90,85}$	TN_{90}
1991	$N_{0,91,91}$	$N_{1,91,90}$	$N_{2,91,89}$	$N_{3,91,88}$	$N_{4,91,87}$	$N_{5,91,86}$	TN_{91}
1992	$N_{0,92,92}$	$N_{1,92,91}$	$N_{2,92,90}$	$N_{3,92,89}$	$N_{4,92,88}$	$N_{5,92,87}$	TN_{92}
1993	$N_{0,93,93}$	$N_{1,93,92}$	$N_{2,93,91}$	$N_{3,93,90}$	$N_{4,93,89}$	$N_{5,93,88}$	TN_{93}
1994	$N_{0,94,94}$	$N_{1,94,93}$	$N_{2,94,92}$	$N_{3,94,91}$	$N_{4,94,90}$	$N_{5,94,89}$	TN_{94}
1995	$N_{0,95,95}$	$N_{1,95,94}$	$N_{2,95,93}$	$N_{3,95,92}$	$N_{4,95,91}$	$N_{5,95,90}$	TN_{95}
1996	$N_{0,96,96}$	$N_{1,96,95}$	$N_{2,96,94}$	$N_{3,96,93}$	$N_{4,96,92}$	$N_{5,96,91}$	TN_{96}

where $N_{x,y,z}$ is the estimated abundance of the *x*th age during the *y*th year, and the *z*th year class or cohort. Note that a diagonal in this matrix follows the abundance of a single cohort over time, and the sum of rows is the total abundance of the stock in a specified year.

A matrix of fishing mortality rates $(F_{x,y,z})$ also results from the sequential population analysis.

Harvest	Fishing Mortality at Age						Total
Year	0	1	2	3	4	5	Fishing Mortality
1990	$F_{0,90,90}$	$F_{1,90,89}$	$F_{2,90,88}$	$F_{3,90,87}$	$F_{4,90,86}$	$F_{5,90,85}$	TF_{90}
1991	$F_{0,91,91}$	$F_{1,91,90}$	$F_{2,91,89}$	$F_{3,91,88}$	$F_{4,91,87}$	$F_{5,91,86}$	TF_{91}
1992	$F_{0,92,92}$	$F_{1,92,91}$	$F_{2,92,90}$	$F_{3,92,89}$	$F_{4,92,88}$	$F_{5,92,87}$	TF_{92}
1993	$F_{0,93,93}$	$F_{1,93,92}$	$F_{2,93,91}$	$F_{3,93,90}$	$F_{4,93,89}$	$F_{5,93,88}$	TF_{93}
1994	$F_{0,94,94}$	$F_{1,94,93}$	$F_{2,94,92}$	$F_{3,94,91}$	$F_{4,94,90}$	$F_{5,94,89}$	TF_{94}
1995	$F_{0,95,95}$	$F_{1,95,94}$	$F_{2,95,93}$	$F_{3,95,92}$	$F_{4,95,91}$	$F_{5,95,90}$	TF_{95}
1996	$F_{0,96,96}$	$F_{1,96,95}$	$F_{2,96,94}$	$F_{3,96,93}$	$F_{4,96,92}$	$F_{5,96,91}$	TF_{96}

Retrospective Models: Length-Based

Length-based retrospective models are adapted from cohort analysis. Length-based cohort analysis (LCA) assumes that the catch taken within a particular size range (lengths) of fish is taken at the mid-point in that size range, and that natural mortality is acting continuously to reduce cohort numbers within the size range (Figure 7).

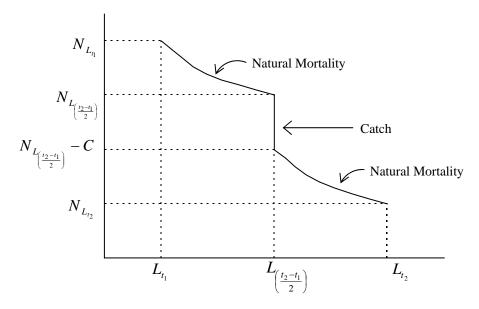


Figure 7. Cohort number as a function of length within a length class, showing Jones' length-based approximation with catch taken instantaneously at mid-length within the range.

LCA requires length composition data for a stock and then assumes that recruitment to the stock has been constant over a period equal to or greater than the life-span of the species. Thus, a pseudo-cohort is formed that is assumed to represent a true cohort or year class. Abundance within each length interval is estimated by:

$$N_{t} = N_{t+\Delta t} e^{M\Delta t} + C_{t} e^{\frac{M\Delta t}{2}}$$

where Δt is the time required to grow from the beginning to the end of a length interval, and Δt is estimated from the rearranged von Bertalanffy growth equation.

$$\Delta t = t_2 - t_1 = \left(\frac{1}{K}\right) \ln \left[\frac{\left(L_{\infty} - L_1\right)}{\left(L_{\infty} - L_2\right)}\right]$$

Computationally, the length intervals are first specified over the full length range of the fish, then the Δt are estimated for each length range. At smaller lengths, the Δt are small, and at larger lengths, the Δt are large. Using the time interval (Δt) for each length interval, the abundance of the pseudo-cohort at the beginning of each length interval is estimated using a rearranged Baranov catch equation. Similarly, fishing mortality in that length range is then estimated using a modified exponential decay equation.

Example 4: Given the following length-based catch history for this pseudo-cohort, length (0-40 cm), K = 1.0, and an assumed natural mortality of 0.7, estimate how many fish initially recruited to the cohort, the cohort abundance trajectory over the length span, and the level of fishing mortality within each size range.

Length	Catch		
40-44	0		
35-39	53		
30-34	88		
25-29	110		
20-24			
15-19			
10-14			
5-9			
0-4			

Total catch:

251 fish over the size range of the cohort

The time interval (Δt) for each length class is estimated using the rearranged von Bertalanffy growth function for the limits of each length class:

Length	Δt	$e^{(M*\Delta t/2)}$
0		
5	0.13	1.0478
10	0.15	1.0554
15	0.18	1.0659
20	0.22	1.0812
25	0.29	1.1059
30	0.41	1.1525
35	0.69	1.2746
39.9	3.91	3.9322

Step (1) The abundance of fish starting the largest length class is estimated using a modified, rearranged Baranov catch equation, and using the catch of the largest length class, the assumed natural mortality (M), and an assumed exploitation ratio (F/Z) for the largest length class of 0.5.

$$N_{35} = {C_{35-39} \brack F_Z}_{(35-39)}$$

$$N_{35} = \frac{53}{0.5} = 106$$

Step (2) The abundance of fish starting the second largest length class is estimated using a Jones length-cohort equation (adapted from the Pope age-cohort equation), and the catch for the second largest length class.

$$N_{30} = \left[N_{35} \left(e^{\left(M * \Delta t /_2 \right)} \right) + C_{(30-34)} \right] e^{\left(M * \Delta t /_2 \right)}$$

$$N_{30} = [106(1.2732) + 88]1.2732$$

$$N_{30} = (224)1.2732 = 284$$

Step (3) The exploitation ratio for the second largest length class is estimated by comparing the abundance of fish starting the largest and second largest length classes, and allowing for catch.

$$(F/Z)_{(30-34)} = {}^{C_{(30-34)}} / (N_{30} - N_{35})$$

$$(F/Z)_{(30-34)} = 88/(284-106) = 88/178 = 0.49$$

Step (4) Fishing mortality for the second largest length class is estimated from the exploitation ratio and the assumed natural mortality.

$$F_{(30-34)} = M \begin{bmatrix} F/Z \\ 1 - F/Z \end{bmatrix}_{(30-34)}$$

$$F_{(30-34)} = 0.7 \left[0.49 / (1 - 0.49) \right] = 0.69$$

Step (5) Abundance of the third largest length class is estimated as in Step (2).

Step (6) Exploitation ratio is estimated as in Step (3).

Step (7) Fishing mortality is estimated as in Step (4).

and so on.

Results:

Length	Catch	Estimated N	Actual N	Estimated F	Actual F
40-44	0		0		0
35-39	53	106	108	0.70	0.70
30-34	88	284	284	0.68	0.70
25-29	110	504	506	0.70	0.70
20-24		617	613	0.00	0.00
15-19		721	720	0.00	0.00
10-14		819	816	0.00	0.00
5-9		913	913	0.00	0.00
0-4		1002	1000	0.00	0.00

Conclusion:

The estimated initial N is 1003 compared to the actual N of 1000; and the estimated F values of 0.69, 0.69, and 0.70 on the exploited size classes compared very well to the actual F values of 0.70.

The form of the complete matrix of input catch at length data for a stock of a relatively short-lived animal is as follows:

Harvest		Total			
Year	25-29	30-34	35-39	40-44	Catch
1990	$C_{25-29,90}$	$C_{30-34,90}$	$C_{35-39,90}$	$C_{40-44,90}$	TC_{90}
1991	$C_{25-29,91}$	$C_{30-34,91}$	$C_{35-39,91}$	$C_{40\text{-}44,91}$	TC_{91}
1992	$C_{25-29,92}$	$C_{30-34,92}$	$C_{35-39,92}$	$C_{40-44,92}$	TC_{92}
1993	$C_{25-29,93}$	$C_{30-34,93}$	$C_{35-39,93}$	$C_{40-44,93}$	TC_{93}
1994	$C_{25-29,94}$	$C_{30-34,94}$	$C_{35-39,94}$	$C_{40\text{-}44,94}$	TC_{94}
1995	$C_{25-29,95}$	$C_{30-34,95}$	$C_{35-39,95}$	$C_{40-44,95}$	TC_{95}
1996	$C_{25-29,96}$	$C_{30-34,96}$	$C_{35-39,96}$	$C_{40-44,96}$	TC_{96}

where $C_{x,y}$ is the catch during the yth year of the xth length interval. Note that a row in this matrix represents the harvest or catch in a given year (y) by length interval (x) and a column in this matrix represents the catch for a specific length interval (x) by year of harvest (y).

Applying sequential population analysis to the previous input catch at length matrix results in output matrices of abundance at length and fishing mortality at length:

Harvest	Abundance at Length									Total Stock
Year	0-4	5-9	10-14	15-19	20-24	25-29	30-34	35-39	40-44	Abundance
1990	$N_{0-4,90}$	$N_{5-9,90}$	$N_{10-14,90}$	$N_{15-19,90}$	$N_{20-24,90}$	$N_{25-29,90}$	$N_{30-34,90}$	$N_{35-39,90}$	$N_{40-44,90}$	TN_{90}
1991	$N_{0-4,91}$	$N_{5-9,91}$	$N_{10-14,91}$	$N_{15-19,91}$	$N_{20-24,91}$	$N_{25-29,91}$	$N_{30-34,91}$	$N_{35-39,91}$	$N_{40-44,91}$	TN_{91}
1992	$N_{0-4,92}$	$N_{5-9,92}$	$N_{10-14,92}$	$N_{15-19,92}$	$N_{20-24,92}$	$N_{25-29,92}$	$N_{30-34,92}$	$N_{35-39,92}$	$N_{40-44,92}$	TN_{92}
1993	$N_{0-4,93}$	$N_{5-9,93}$	$N_{10-14,93}$	$N_{15-19,93}$	$N_{20-24,93}$	$N_{25-29,93}$	$N_{30-34,93}$	$N_{35-39,93}$	$N_{40-44,93}$	TN_{93}
1994	$N_{0-4,94}$	$N_{5-9,94}$	$N_{10-14,94}$	$N_{15-19,94}$	$N_{20-24,94}$	$N_{25-29,94}$	$N_{30-34,94}$	$N_{35-39,94}$	$N_{40-44,94}$	TN_{94}
1995	$N_{0-4,95}$	$N_{5-9,95}$	$N_{10-14,95}$	$N_{15-19,95}$	$N_{20-24,95}$	$N_{25-29,95}$	$N_{30-34,95}$	$N_{35-39,95}$	$N_{40-44,95}$	TN_{95}
1996	$N_{0-4,96}$	$N_{5-9,96}$	$N_{10-14,96}$	$N_{15-19,96}$	$N_{20-24,96}$	$N_{25-29,96}$	$N_{30-34,96}$	$N_{35-39,96}$	$N_{40-44,96}$	TN_{96}

where $N_{x,y}$ is the estimated abundance during the yth year of the xth length interval.

A matrix of fishing mortality rates $(F_{x,y})$ also results from the sequential population analysis.

Harvest	Fi	Fishing Mortality at Length						
Year	25-29	30-34	35-39	40-44	Mortality			
1990	$F_{25-29,90}$	$F_{30-34,90}$	$F_{35-39,90}$	$F_{40-44,90}$	AF_{90}			
1991	$F_{25-29,91}$	$F_{30-34,91}$	$F_{35-39,91}$	$F_{40\text{-}44,91}$	AF_{91}			
1992	$F_{25-29,92}$	$F_{30-34,92}$	$F_{35-39,92}$	$F_{40-44,92}$	AF_{92}			
1993	$F_{25-29,93}$	$F_{30-34,93}$	$F_{35-39,93}$	$F_{40-44,93}$	AF_{93}			
1994	$F_{25-29,94}$	$F_{30-34,94}$	$F_{35-39,94}$	$F_{40\text{-}44,94}$	AF_{94}			
1995	$F_{25-29,95}$	$F_{30-34,95}$	$F_{35-39,95}$	$F_{40-44,95}$	AF_{95}			
1996	$F_{25-29,96}$	$F_{30-34,96}$	$F_{35-39,96}$	$F_{40-44,96}$	AF_{96}			

Exercises

1. The following catches were taken over the early portion of the lifespan of a cohort of fish in a pond.

Age	Catch
1	100
2	500
3	300
4	200

The fishing mortality rate on the oldest age (F_4) is estimated to be 0.5 and the natural mortality rate is constant over all ages at M = 0.5.

- (a) Determine the population size and the fishing mortality rate for this population using the cohort analysis approximation.
- (b) If the fishing mortality rate on the oldest age is now assumed to be $F_4 = 0.6$, what effect does this have on the estimates?
- (c) If the natural mortality rate on ages 1 and 2 is found to be M = 0.7 and that on all other ages is M = 0.4, what effect does this have on the estimates?
- 2. Given a catch-at age matrix (nine age classes) for mid-Atlantic bluefish for the period 1982-1996 and an assumed natural mortality of 0.25, abundance-at-age and fishing mortality rate-at-age matrices for bluefish were developed using cohort analysis due to its computational simplicity.
 - (a) Investigate the sensitivity of the estimated population structure in 1995 to changes in the assumed value of natural mortality over a range of values of *M* from 0.2 to 0.4 in units of 0.02.
 - (b) Investigate the sensitivity of the exploited population structure in 1995 to the solution of terminal F values. Use the following starting F values: $F_{0,96} = 0.01$ and $F_{1,96} \rightarrow F_{9,96} = 0.3$ for 1996.

M 0.25

				Cat	ch at Ag	ge (milli	ons)			
Year	0	1	2	3	4	5	6	7	8	9
1982	7.001	12.493	4.633	2.504	2.297	2.418	1.368	1.050	0.538	0.281
1983	6.784	8.526	9.447	2.605	1.611	1.840	1.818	1.710	0.752	0.325
1984	8.719	8.405	4.060	3.184	1.462	1.491	1.679	2.053	0.751	0.237
1985	6.022	5.282	7.526	2.734	1.711	1.036	0.733	1.038	0.405	0.213
1986	5.194	5.546	9.470	6.471	2.900	2.551	2.047	1.641	0.770	0.289
1987	6.416	6.026	4.686	5.480	3.644	2.127	1.718	1.333	0.528	0.105
1988	1.633	3.780	2.147	1.876	3.300	1.590	1.332	0.783	0.315	0.095
1989	6.102	6.599	2.368	1.025	1.261	1.586	0.887	0.606	0.265	0.103
1990	1.718	10.695	3.739	0.572	0.533	1.171	1.000	0.430	0.173	0.057
1991	4.098	7.075	7.569	2.420	0.612	1.732	1.523	0.989	0.165	0.041
1992	0.882	6.932	4.621	4.527	1.256	1.005	1.348	0.632	0.242	0.067
1993	0.648	4.217	1.463	1.729	2.224	0.396	0.485	0.486	0.117	0.025
1994	1.967	6.449	1.806	0.670	1.264	0.899	0.370	0.339	0.221	0.104
1995	0.382	5.906	2.745	0.491	0.838	1.801	0.602	0.357	0.148	0.045
1996	1.664	3.584	2.528	1.105	0.405	0.741	0.892	0.447	0.231	0.042

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Chapter XI

BIOLOGICAL REFERENCE POINTS USED IN FISHERIES MANAGEMENT: DEFINITIONS AND METHODOLOGY

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Introduction

A variety of fish stock assessment models are used to assess the status of a fish stock and the intensity of harvesting activity on that stock. The models range in complexity from conceptually and mathematically simple index models to computer intensive age- or length-structured models. The data requirements of the models also vary from simple to complex. The output of the models provides both an understanding of fish stock dynamics and reference points that are used in fisheries management.

Reference points are designed to provide objective criteria against which to evaluate the current status of a fish stock and levels of mortality. Reference points are used to determine whether a fish stock is "overfished" (*i.e.* biomass is below a minimum level necessary to maintain the stock), or if "overfishing" is occurring on a fish stock (*i.e.* the level of fishing mortality exceeds a specified level that allows for sustainable production). Reference points also provide insight into optimum harvesting strategies that maximize sustainable yield from a fish stock by identifying the optimum fish size or age to target, and level of fishing mortality required.

Unfortunately, there are sources of error and uncertainty incorporated into the parameters (including reference points) used to describe stock status and fishing mortality (Fogarty et al. 1996). These are due to stochasticity inherent in the process being observed, error in the measurement of the process, and a lack of understanding of the complexity of the processes. As a result of this uncertainty, it is necessary to understand and quantify risk in fisheries management, which can be defined as the probability that exploitation will exceed a threshold level where the long-term sustainability of a fish stock is threatened. Precaution is required in our approach to management actions, and fishery managers should be conservative when developing management advice.

Overfishing reference points are divided into target and threshold or limit reference points. Target reference points indicate a state of the resource and/or fishing which is considered to be desirable, and at which management should aim. Threshold/limit reference points indicate a maximum fishing mortality or minimum stock biomass beyond which is deleterious to the stock and fishery and which management action should avoid. The difference between targets and limits is due not only to biological characteristics of the species, but also the uncertainty in our measurements and calculations.

Index Data

Research vessel or other resource survey data (mean catch per tow for a net and mean catch per set for traps), or fishery catchperunit effort (CPUE) data can both be used as an index of relative stock abundance (Figure 1).

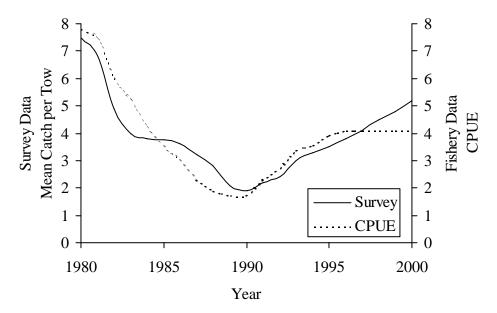


Figure 1. Indices of relative abundance based on survey and fishery data.

Index models are simple and require minimal data, but also provide minimal understanding of fish stock structure and dynamics, and little ability to forecast future trends in catch or abundance. Despite their apparent simplicity, index models are subject to uncertainty due problems such as errors in landings or fishery effort data, changes in data collection protocol, and changes in environmental conditions that can lead to changes in catchability.

Survey indices can be adjusted to absolute indices if the efficiency of the sampling gear can be determined, and the area sampled is scaled to the stock area. For example, scientific dredge survey data can be adjusted by first determining the area swept by the tow of the dredge (the product of dredge width and distance towed). The stock area is then divided by the swept area, and this is multiplied by the mean survey catch per tow. Finally, this must be adjusted by the efficiency of the gear as determined in a depletion experiment or other techniques.

Yield per Recruit Models

Yield per recruit (YPR) models provide evaluations of yield as a function of fishing mortality and age or size of entry into the fishery, incorporating information on biological parameters (growth, weight at age, and natural mortality rates). The YPR models provide two important reference points and a growth overfishing definition (Figure 2).

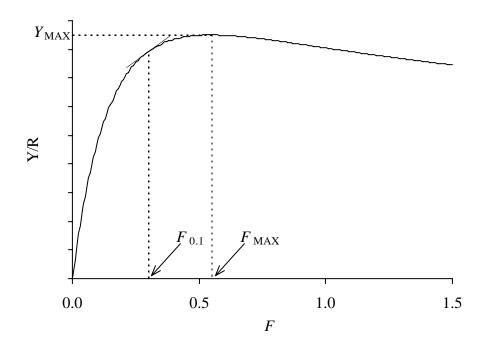


Figure 2. Y/R model showing Y_{MAX} , F_{MAX} , and $F_{0.1}$.

 Y_{MAX} is the maximum yield that can be removed from a cohort, given a specific age or size of entry into the fishery and the biological parameters of the fish stock.

 F_{MAX} is the fishing mortality rate that provides Y_{MAX} , and is now considered a threshold or limit reference point.

 $F_{0.1}$ is a fishing mortality rate on the YPR curve at which the slope of the curve is 10% (0.1) of the slope of the curve at the origin. The $F_{0.1}$ measure, although arbitrary, is a target reference point, and also represents a bioeconomic reference point, in that additional increases in F only marginally contribute to yield.

Growth overfishing occurs at fishing mortality rates greater than $F_{\rm MAX}$ because overall yield is reduced, despite increased effort. The fishery is removing too many fish before the population reaches the maximum growth potential, thus reducing yield. Growth overfishing, although not usually biologically problematic on its own, is economically harmful to the fishing industry.

Spawning Stock Biomass and Egg per Recruit Models

Spawning stock biomass (SSBPR or SPR) and egg (EPR) per recruit models are corollaries to YPR models. The calculations are analogous to YPR models with the addition of maturation and fecundity data. These models provide evaluations of spawning stock biomass or egg production as a function of fishing mortality. Both SPR and EPR models generally express fishing mortality as a percentage (" $F_{x\%}$ ") of the spawning stock biomass or egg production in the absence of fishing (F = 0.0). The SPR and EPR models provide both target and threshold limit reference points, and a recruitment overfishing definition (Figure 3).

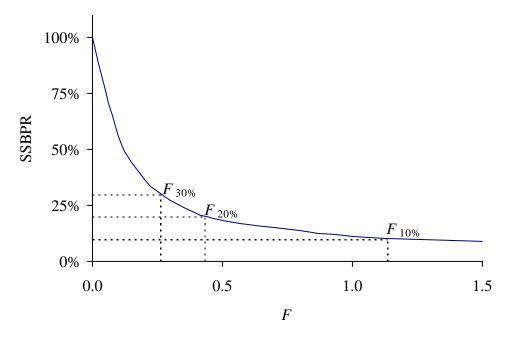


Figure 3. SSB/R model showing $F_{10, 20, \text{ and } 30\%}$.

 $F_{\rm x\%}$ reference point is selected at a fishing level (i.e. X% of spawning potential) that allows sufficient recruitment to ensure sustainable exploitation of the stock. The selection of a particular percentage value is related to the steepness of the stock-recruitment relationship near the origin (low stock sizes), and the biological characteristics of the stock. Long-lived, slow growing species can accommodate lower levels of percent spawning stock remaining ($F_{10-20\%}$), compared to short-lived, fast growing species that require higher levels of spawning stock remaining ($F_{20-40\%}$). Generally the target reference point is 5-10% higher than threshold or limit reference points.

The $F_{x\%}$ reference points are related to recruitment overfishing. Exceeding a particular $F_{x\%}$ indicates that there will not be sufficient spawning biomass available for future reproduction, leading to recruitment failure.

Surplus Production Models

Surplus production models utilize catch and relative abundance indices to generate estimates of exploitation rate, fishery yield stock abundance and maximum sustainable yield at particular levels of stock size and fishing effort. The reference points generated from surplus production models are conceptually simple, but are based on assumed equilibrium conditions for the stock that may not exist. These models can provide both target and threshold/limit reference points, as well as bioeconomic and overfishing reference points.

The yield-stock biomass model (Figure 4) relates fishery catch data in a given year to estimates of stock biomass in that year, providing both target and limit/threshold reference points.

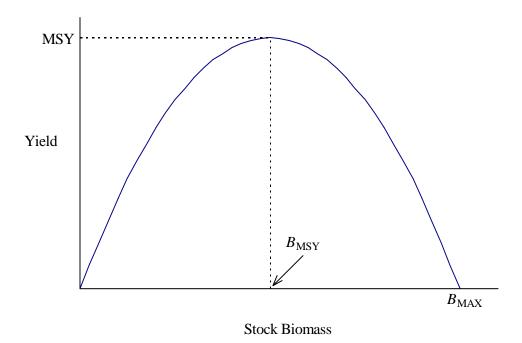


Figure 4. Yield-stock biomass model showing MSY and B_{MSY} .

MSY is the maximum sustainable yield from the stock under existing conditions. Using the Schaefer surplus production model, MSY is equal to $(B_{\text{MAX}} * r)/4$ where r is the intrinsic growth rate of the population.

 $B_{\rm MAX}$ is the virgin biomass of the stock at carrying capacity under existing conditions.

 B_{MSY} is the stock size (biomass) that produces MSY. Using the Schaefer surplus production model, B_{MSY} is ½ the virgin biomass.

 $B_{\rm MSY}$ is regarded as a limit or threshold reference point representing the minimum acceptable level of biomass for a managed stock. A target biomass level is greater than $B_{\rm MSY}$.

Exploitation rate at MSY is equal to r/2.

Surplus production models can also be used to estimate the effort required to achieve MSY called f_{MSY} (Figure 5). To calculate f_{MSY} , divide r by 2*q, where q is catchability of the abundance index. $f_{2/3\text{MSY}}$ (two-thirds the value of f_{MSY}) has been suggested as a reference point because it provides a substantial decrease in effort that should still result in 90+% of the MSY. f_{MSY} is considered a limit reference point, while $f_{2/3\text{MSY}}$ is a target reference point. Fishing at effort levels greater than f_{MSY} results in overfishing.

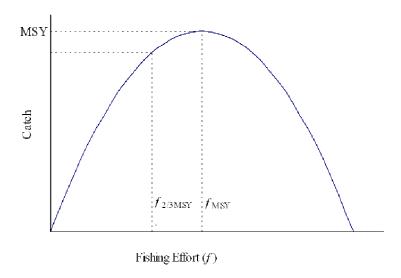


Figure 5. Fishing effort-yield curve showing $f_{
m MSY}$ and $f_{
m 2/3MSY}$ reference points.

Finally, surplus production models can be used to represent bioeconomic conditions in a fishery where a linear cost function is added to the catch-fishing effort model (Figure 6). MEY is the largest positive difference between revenue and cost (*i.e.* where profits are maximized). Note that when costs exceed revenue due to excessive effort, the fishery ceases to be profitable, and operates at a loss.

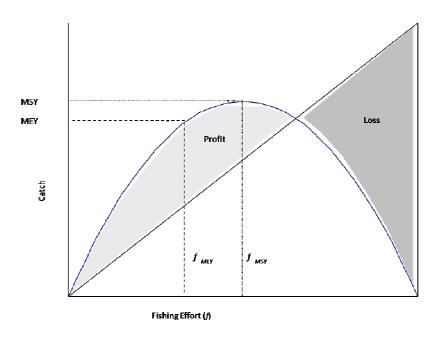


Figure 6. Fishing effort-yield curve and cost function showing maximum economic yield and the f_{MEY} reference point.

Stock-Recruitment Models

Stock-recruitment (*S-R*) models utilize paired data on spawning stock numbers and the resulting number of recruits to the fishery with the appropriate time lag. *S-R* models are important in fisheries management because they provide information on minimum spawning stock size needed to avoid recruitment failure, and the stock size that provides maximum surplus reproduction (Figure 7).

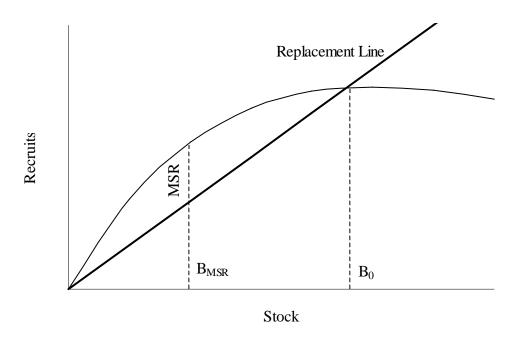


Figure 7. Stock-recruitment relationship showing $B_{\rm MSR}$ and B_0 .

Recruits (number/biomass) exceed stock (number/biomass) up to the point where the replacement function intersects the S-R function. This point is referred to as B_0 . Maximum surplus reproduction (MSR) occurs at $B_{\rm MSR}$, where the difference between the S-R function and the replacement function is maximized.

Age and Length Structured Models

Age and length structured models include the analysis of the observed length or age composition of the catch and biological information to provide estimates of fishing mortality, total abundance, and spawning stock abundance over time. Resulting estimates can be combined with estimates of incoming recruitment from research vessel surveys or other sources to make predictions of catch and stock size in future years in relation to fishing mortality. Most age and length structured models offer no specific biological reference points on their own; however, some new formulations of statistical catch-at-age models allow for MSY reference points to be estimated within the model itself (Martell et al. 2008). Typically, output from an age-structured model is used as input to a yield- or SSB-per-recruit model to obtain reference points for the stock assessment.

Integrating Models

Spawning stock per recruit (SPR) and stock-recruitment (S-R) models can be integrated to provide insight into stock dynamics and biological reference points (Figure 8).

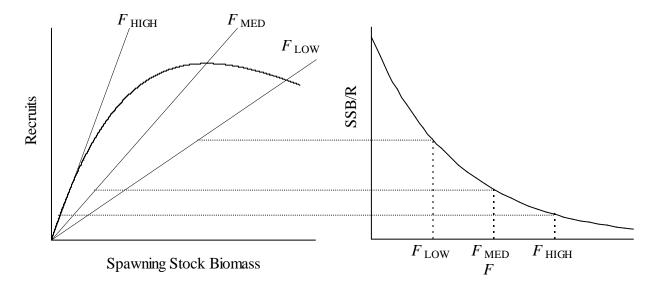


Figure 8. Integrated S-R and SSB/R plots.

Based on the SPR plot, for any given level of fishing mortality, the survival ratio (R/S) is estimated from the reciprocal of the SPR. That is, the slope of the straight line shown on the S-R plot is the inverse of the SPR, which corresponds to a specified F level. The predicted S-R function is a best fit of the model to data points that relate paired stock-recruitment observations. The intersections of the R/S linear functions with the predicted S-R function represent potential equilibrium points for the fishery. A biological reference point F_{MED} or F_{REP} represents the fishing mortality rate that allows the stock to replace itself (new recruitment equally replaces the spawning stock). At this level of fishing mortality current stock levels will be sustained. This point is determined by dividing the observed S-R data points, so that 50% of the observed data points are above the R/S line and 50% of the observed data points are below the line. Thus, the S/R line represents the median fishing mortality rate (F_{MED}) that results in an average survival ratio (S/R) = 1, at which the stock replaces itself. Other related biological reference points are F_{LOW} and F_{HIGH} that are based on 90% and 10% of the S-R data points above the line through the origin corresponding to that level of mortality. F_{LOW} indicates a low probability of stock decline, and some likelihood of stock increase. F_{HIGH} indicates a high probability that fishing at this level will result in stock declines.

Surplus production and YPR models with their related exploitation and fishing mortality rate reference points can also be integrated into the *S-R* and SPR models to provide a single species theory of fishing (Sissenwine et al. 1988).

Control Rules

For federal fisheries in the United States, overfishing definitions were developed in the 1980s to address two of the national standards identified in the Magnuson Fishery Conservation and Management Act (MFCMA). National Standard 1 required conservation and management measures to prevent overfishing. National Standard 2 required that the best scientific information available be used as a basis for conservation and management measures. In 1989, the 602 Guidelines were published in the Federal Register (CFR) to detail what would be needed in each fishery management plan (FMP) in order to define overfishing with respect to these standards. In the 1990s, the Magnuson-Stevens Fishery Conservation and Management Act (MSFCMA) and Sustainable Fisheries Act (SFA) resulted in the development of new guidelines. These guidelines specify the use of "control rules" in an FMP.

Harvest control rules are pre-agreed upon protocols that control fishing mortality with respect to stock status and the limit/threshold reference points. The control rules incorporate minimum biomass and maximum fishing mortality thresholds, as well as targets for these parameters, and rebuilding horizons for overfished stocks that include biomass and fishing mortality schedules. Control rules also specify optimum harvest strategies to achieve maximum sustainable yield (MSY) from the stock under prevailing ecological and environmental conditions (Figure 9).

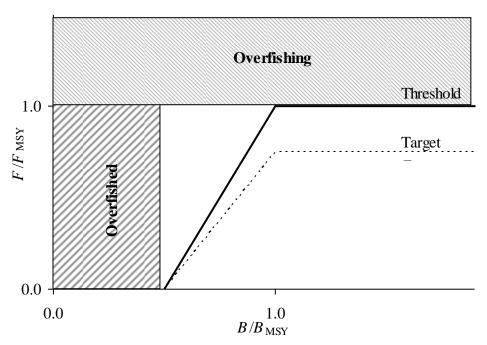


Figure 9. Harvest control rule based on biomass levels relative to $B_{\rm MSY}$ and fishing mortality rates relative to $F_{\rm MSY}$.

Optimum yield from a fishery stock will be sustainably achieved when existing biomass exceeds B_{MSY} ($B/B_{\text{MSY}} \ge 1$) and when fishing mortality is less than F_{MSY} ($F/F_{\text{MSY}} \le 1$).

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