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INTRODUCTION TO FISH STOCK ASSESSMENT, FISHERIES MANAGEMENT, FISHERIES AND FISHERY-DEPENDENT DATA, AND RESEARCH SURVEYS AND FISHERY-INDEPENDENT DATA

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Background

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.

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 Act has many standards it attempts to achieve, including promote conservation and utilization of the fishery resources based on the best scientific information available, seek to promote optimum sustainable yield while preventing overfishing, and protect the habitats for fishery resources. The full text can be found at www.nmfs.gov/sfa/magact.

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 which 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 State 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. Recently, these commissions were charged by Congress to promote and encourage management of interjurisdictional marine resources.

The Atlantic Coastal Fisheries Cooperative Management Act passed by Congress in 1993 charged the ASMFC with the responsibility of developing FMPs for transboundary, migratory coastal species. For example, in 1998, the ASMFC developed a FMP for American lobster, a resource harvested from Maine to Virginia.

The main management strategies used to control harvest rates include restricting effort and restricting harvest. 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 (i.e. restricting harvest). These quotas result in “derby fisheries” where individual fishermen attempt to catch as much as they can, as quickly 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). After controlling access to the fishery with a moratorium on new licenses, fishermen are individually awarded a portion or allocation of the TAC each year, and that share is transferable to other fishermen via direct sale. Thus larger, more efficient harvesters are able to purchase 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.

**Fish Stock Assessment**

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:

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. Population and fishery parameters that may include stock-recruitment relationships, estimation of exploitation rates, yield per recruit and spawning stock/egg per recruit models, surplus production models, and stock abundance indices.

5. Biological reference points based on the previous models and analyses.

6. Review of management objectives and alternative actions to achieve a sustainable fishery.

**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. 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; it is 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, which 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).](image)

On the east coast of the U.S., 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 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.

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 to the 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 (Sundstrom 1957).

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 than 100 m in length 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.

![Oyster dredge](image)

**Figure 4.** Oyster dredge (Sundstrom 1957).

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 (Sundstrom 1957).

Bottom trawl fisheries are prosecuted for demersal species on all coasts of the U.S. 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 seafloor 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 (Sundstrom 1957).](image)

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.
**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 (Sundstrom 1957).](image)

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, or other means. However, landings data may not be entirely representative of the actual 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 often based on license data according to gear type, vessel tonnage, days at sea or fishing, or the amount of gear set and soak time. 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. An example of fishery-dependent data can be seen in Figure 8. The Potomac River blue crab harvest time series of both catch and effort was obtained from historical commercial harvest and license data from the Potomac River Fisheries Commission.

Figure 8. Potomac River blue crab harvest and licenses issued.

Recreational fisheries landing statistics are collected by port-based samplers who conduct intercept interviews with fishermen returning from a day of fishing at sea. These data are supplemented with the Marine Recreational Fishery Statistics Survey (MRFSS). The MRFSS is
a series of surveys initiated by NMFS starting in 1979 to obtain standardized and comparable estimates of participation, effort, and catch by recreational anglers in the marine waters of the United States. The MRFSS collects recreational fisheries data using both dockside intercept and telephone surveys. The intercept survey collects data on the number, weights, and lengths of fish caught by species, state and county of residence, and avidity level (e.g. trips per year, mode of fishing, and primary area of fishing). The telephone survey collects data on the presence of marine recreational anglers in the household, number of anglers per household, number of fishing trips in a 2-month period, the mode of each trip, and the locations (county) of each trip. The estimated number of marine recreational fishing trips in Rhode Island from the MRFSS Survey can be seen in a time series of recreational effort (Figure 9).

![Figure 9. Estimated number of marine recreational fishing trips in Rhode Island from MRFSS Survey.](image)

Research Surveys

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, and other life history characteristics, 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 within 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.
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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 \( x \).

A linear function can be described by:

\[
y = ax + b,
\]

where \( a \) and \( b \) are constants (Figure 2).
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 $b = 0$ ($y = ax; \text{i.e., the function intersects the origin}$), (Figure 3a) and when $a = 1$ and $b = 0$ ($y = x$) (Figure 3b).

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 $a < 0$. 

\[ y = ax + b \]

Figure 2. Linear function: $y = ax + b$.
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: $y = -Ax^2 + Abx$.](image)

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: $y = a^x$.](image)
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: \( y = 1 - e^{-x} \).](attachment:image.png)

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.


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:

\[
\begin{align*}
    a^0 &= 1 \\
    a^{-M} &= \frac{1}{a^M} \\
    (a^N)(a^M) &= a^{(N+M)} \\
    \left(\frac{a^N}{a^M}\right) &= a^{(N-M)} \\
    (a^M)(b^M) &= (a \cdot b)^M \\
    (a^M)(b^M) &= \left(\frac{a}{b}\right)^M \\
    (a^N)^M &= a^{NM} \\
    a^{M/N} &= \sqrt[N]{a^M}.
\end{align*}
\]

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

\[
y = x^N.
\]
\[ y = a^x. \]

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

\[
e = \lim_{h \to \infty} \left(1 + \frac{1}{h}\right)^h = 1 + \left(\frac{1}{1!}\right) + \left(\frac{1}{2!}\right) + \left(\frac{1}{3!}\right) + \ldots = 2.7182
\]

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:

\[
\log_{10} 10 = 1 \\
\log_e e = \ln e = 1 \\
\log_{10} 1 = \ln 1 = 0 \\
\log_a (x) + \log_a (y) = \log_a (x \cdot y) \\
\log_a (x) - \log_a (y) = \log_a \left(\frac{x}{y}\right) \\
\log_a \left(x^M\right) = M \log_a (x).
\]

**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

$$y = b - ax$$

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

$$\frac{y}{x} = b - ax$$
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 11b). The following are functions and their derivatives:

<table>
<thead>
<tr>
<th>Function</th>
<th>Derivative</th>
</tr>
</thead>
<tbody>
<tr>
<td>( a ) (constant)</td>
<td>0</td>
</tr>
<tr>
<td>( ax )</td>
<td>( a )</td>
</tr>
<tr>
<td>( ax^n )</td>
<td>( aNax^{n-1} )</td>
</tr>
<tr>
<td>( \ln x )</td>
<td>( \frac{1}{x} )</td>
</tr>
</tbody>
</table>

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:

\[
\frac{dy}{dx} \quad \text{or} \quad y' = f'(x).
\]

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.
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),

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

\[ b = 2ax \]

\[ x = \frac{b}{2a} \cdot \]

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

\[ y = b \left( \frac{b}{2a} \right) - a \left( \frac{b}{2a} \right)^2 \]

\[ y = \frac{b^2}{2a} - \frac{ab^2}{4a^2} \]

\[ y = \frac{2b^2}{4a} - \frac{b^2}{4a} = \frac{b^2}{4a} \cdot \]

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

\[ x = \frac{b}{2a} \]

\[ y = \frac{b^2}{4a} \cdot \]

**Figure 13.** Functions: (a) \( y = bx - ax^2 \)

(b) \( y' = b - 2ax \).
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: \( y = f(x) \).](image)

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

\[
\int_{x=a}^{b} f(x) \, dx = [F(x)]_{a}^{b} = F(b) - F(a)
\]

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:

\[ \int ax \, dx = ax \]
\[ \int af(x) \, dx = a \int f(x) \, dx \]
\[ \int x^M \, dx = \frac{x^{M+1}}{M+1} \quad M \neq -1 \]
\[ \int a^x \, dx = \frac{a^x}{\ln(a)} \quad a > 0, a \neq 1 \]
\[ \int e^{ax} \, dx = \frac{e^{ax}}{a} \]
\[ \int \frac{1}{x} \, dx = \ln(x) \]
\[ \int \ln(x) \, dx = x \ln(x) - x \]
\[ \int [f(x) + g(x)] \, dx = \int f(x) \, dx + \int g(x) \, dx \]
\[ \int f(x)g'(x) \, dx = f(x)g(x) - \int f'(x)g(x) \, dx. \]

**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:

\[ \int_2^4 \left(3x^2 + 5\right) \, dx = \left[x^3 + 5x\right]_2^4 \]

\[ = (64 + 20) - (8 + 10) = 66. \]

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:

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

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:

$$\frac{1}{y} \ dy = adx.$$  

Integrating both sides of the equation:

$$\int \frac{1}{y} \ dy = \int adx$$

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

Evaluating the integrals and rearranging:

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

$$\ln(y_f) - \ln(y_0) = ax.$$
\[ \ln\left(\frac{y(x)}{y(0)}\right) = ax \]
\[ \frac{y(x)}{y(0)} = e^{ax} \]
\[ y(x) = y(0)e^{ax} . \]

Applying this solution technique to the population rate equation:

\[ \frac{dN}{dt} = -ZN \]
\[ \frac{1}{N} \frac{dN}{dt} = -Z \, dt \]
\[ \ln \left. N(t) \right|_{N_0}^{N_t} = -Z \int_0^t dt \]
\[ \ln(N_t - N_0) = -Zt - Z \cdot 0 \]
\[ N_t = N_0e^{-Zt} . \]

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 provides the original differential equation

\[ \frac{d}{dt}(N_t) = \frac{d}{dt}(N_0e^{-Zt}) \]
\[ \frac{dN_t}{dt} = N_0e^{-Zt}(-Z) . \]

Substituting
\[ N_0 = N_t e^{Zt} \]
yields:
\[ \frac{dN_t}{dt} = N_t (-Z) \]
\[ \frac{dN}{dt} = -ZN . \]

**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:
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: \( s^2 = \frac{1}{n-1} \sum_{i=1}^{n} (x_i - \bar{x})^2 \)

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

Standard Error: \( S.E. = \frac{s}{\sqrt{n}} \).

The Coefficient of Variation (\( C.V. \)) is a measure of variability relative to the mean
\[
C.V. = \frac{s}{\bar{x}}.
\]

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

\[
\begin{array}{ccc}
15.5 & 18.2 \\
16.3 & 19.3 \\
18.3 & 17.9 \\
17.3 & 16.5 \\
15.8 & 20.4 \\
14.9 & 17.8 \\
16.7 & 19.7 \\
17.3 & 18.4 \\
16.2 & 18.6 \\
17.8 & 17.4 \\
\end{array}
\]

Calculating the descriptive statistics provides:

Sample size = \( n = 20 \)
Mean = $\bar{X} = 17.5$ cm

Variance = $s^2 = 2.0$ cm$^2$

Standard Deviation = $s = 1.4$ cm

$$C.V. = \frac{s}{\bar{X}} = \frac{1.4}{17.5} = 0.08$$

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.

<table>
<thead>
<tr>
<th>Group</th>
<th>Number of Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>14</td>
<td>1</td>
</tr>
<tr>
<td>15</td>
<td>2</td>
</tr>
<tr>
<td>16</td>
<td>4</td>
</tr>
<tr>
<td>17</td>
<td>6</td>
</tr>
<tr>
<td>18</td>
<td>4</td>
</tr>
<tr>
<td>19</td>
<td>2</td>
</tr>
<tr>
<td>20</td>
<td>1</td>
</tr>
</tbody>
</table>

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:

\[ \text{C.I.} = \bar{x} \pm t_{(n-1)\alpha/2} \left( \frac{1}{n} \right)^{1/2} \left( S.E. \right) \]

where \( \bar{x} \) 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-\( \alpha \).

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

\[ 17.5 \pm (2)(0.32) = 17.5 \pm 0.64 = 16.9 \leq \bar{x} \leq 18.1 \text{ cm.} \]

**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

\[ 16.4 \pm 0.60 = 15.8 \leq \bar{x} \leq 17.0 \text{ cm.} \]

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).
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.

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:

<table>
<thead>
<tr>
<th>$W$ (gr)</th>
<th>$L$ (cm)</th>
<th>$\ln(W)$</th>
<th>$\ln(L)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>9710</td>
<td>100</td>
<td>9.18</td>
<td>4.61</td>
</tr>
<tr>
<td>6020</td>
<td>85</td>
<td>8.70</td>
<td>4.44</td>
</tr>
<tr>
<td>3610</td>
<td>72</td>
<td>8.19</td>
<td>4.28</td>
</tr>
<tr>
<td>2620</td>
<td>65</td>
<td>7.87</td>
<td>4.17</td>
</tr>
<tr>
<td>1150</td>
<td>50</td>
<td>7.05</td>
<td>3.91</td>
</tr>
<tr>
<td>680</td>
<td>42</td>
<td>6.52</td>
<td>3.74</td>
</tr>
<tr>
<td>360</td>
<td>35</td>
<td>5.89</td>
<td>3.56</td>
</tr>
</tbody>
</table>

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

$$a' = -5.1949$$
$$b' = 3.1273.$$  

The non-linear 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) models for the weight-length relationship: $W = 0.005545L^{3.1273}$. 

---

II - 20
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.

<table>
<thead>
<tr>
<th>(x)</th>
<th>5</th>
<th>10</th>
<th>15</th>
<th>20</th>
<th>25</th>
<th>30</th>
</tr>
</thead>
<tbody>
<tr>
<td>(y)</td>
<td>17</td>
<td>32</td>
<td>45</td>
<td>65</td>
<td>57</td>
<td>72</td>
</tr>
</tbody>
</table>

2. Calculate the following.

\[10^3\quad 10^{-1}\quad 4^0\quad 8^{2/3}\quad 25^{-1/2}\]

3. Calculate the following.

\[
\log_{10}(42.5)\quad \ln(2.52)
\]

4. Determine the value of \(x\).

\[0.70 = e^{-x}\quad 10^4 = e^x\]

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.

\[
\int_{1}^{2} x^2 \, dx \\
\int_{0}^{2} e^x \, dx \\
\int_{2}^{4} (3 + 2x) \, dx
\]
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.

<table>
<thead>
<tr>
<th>Length (cm)</th>
<th>10</th>
<th>15</th>
<th>20</th>
<th>25</th>
<th>30</th>
<th>35</th>
<th>40</th>
<th>45</th>
<th>50</th>
</tr>
</thead>
<tbody>
<tr>
<td>Group A</td>
<td>3</td>
<td>7</td>
<td>18</td>
<td>29</td>
<td>21</td>
<td>12</td>
<td>6</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Group B</td>
<td>0</td>
<td>5</td>
<td>12</td>
<td>23</td>
<td>32</td>
<td>15</td>
<td>7</td>
<td>2</td>
<td>1</td>
</tr>
</tbody>
</table>
Bibliography


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 \( (\text{Figure 1}) \). 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 \( (\text{Figure 2}) \).

![Figure 1. Growth curve for length where \( L_\infty \) is the maximum length that can be achieved.](image_url)

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 \( (\text{e.g., for} \) ...
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 $W_\infty$ 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):

$$\frac{dL}{dt} = KL - KL_t$$

where $L_\infty$ 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).](image)

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 

$b \equiv KL_\infty$.

The growth rate equation is a differential equation that is solved by the separation of variables technique. Rearranging and integrating yields:
\[
\int \left[ \frac{1}{(L_\infty - L_t)} \right] dL = \int K dt.
\]

Based on integral tables,
\[
- \ln \left[ L_\infty - L_t \right]_{t_0}^{t} = K t \bigg|_{t_0}^{t}.
\]

Assuming \( t_0 = 0 \) and \( L_0 = 0 \) and substituting,
\[
- \ln \left[ \frac{L_\infty - L_t}{L_\infty} \right] = K t.
\]

Taking the inverse natural log, or exponential, and rearranging yields:
\[
\frac{L_\infty - L_t}{L_\infty} = e^{-Kt}
\]
\[
L_\infty - L_t = L_\infty e^{-Kt}
\]
\[
-L_t = L_\infty e^{-Kt} - L_\infty
\]
\[
L_t = L_\infty (1 - e^{-Kt}).
\]

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):

\[
L_t = L_\infty (1 - e^{-K(t-t_0)}).
\]

---

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

**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:

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

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

\[ \frac{\Delta L}{\Delta t} = KL_{\infty} - KL_t, \]

which has the form of the linear model:

\[ y = b + ax, \]

where \(K = \text{slope}\), \(L_{\infty} = \text{y-intercept}/K\).

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, calculate the von Bertalanffy growth model parameters using the Gulland-Holt method.
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 $KL_\infty$ which in this example equals 22.6 cm. Therefore,

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

\begin{table}
\begin{tabular}{|c|c|c|c|}
\hline
Age (t) & Length (cm) ($L_t$) & Growth Increment (cm) ($L_{t+1} - L_t$) & Mean Length (cm) ($\frac{L_{t+1} + L_t}{2}$) \\
\hline
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 & & \\
\hline
\end{tabular}
\end{table}

\textbf{Figure 7. Gulland-Holt plot of growth rate against mean length.}

The $x$-axis intercept (i.e., when $\left(\frac{\Delta L}{\Delta t}\right) = 0$), is a verification of the value of $L_\infty$. 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:

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

and for $t = 2$ and $L_t = 36$,
The mean $t_0$ is -0.495.

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

\[
K = 0.4 \\
L_\infty = 56.5 \text{ cm} \\
t_0 = -0.495.
\]

**Ford-Walford Plot**

An alternative method to determine the parameters $K$ and $L_\infty$ 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 $t+T$:

\[
L_t = L_\infty \left(1 - e^{-Kt}\right) \quad \text{and} \quad L_{t+T} = L_\infty \left(1 - e^{-K(t+T)}\right).
\]

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

\[
L_{t+T} - L_t = L_\infty \left[1 - e^{-K(t+T)}\right] - L_\infty \left[1 - e^{-Kt}\right] \\
L_{t+T} - L_t = L_\infty e^{-Kt} \left[1 - e^{-KT}\right] \\
L_{t+T} = L_\infty e^{-Kt} \left[1 - e^{-KT}\right] + L_t.
\]

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

\[
L_{t+T} = -(L_t - L_\infty) \left(1 - e^{-KT}\right) + L_t \\
L_{t+T} = L_\infty \left(1 - e^{-KT}\right) + L_t e^{-KT}.
\]

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 $b = L_\infty \left(1 - e^{-KT}\right)$. 

---

III - 8
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 $L_\infty$.

![Figure 8. Ford-Walford plot of growth at time $t+T$ versus length at time $t$.](image)

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 $L_\infty$.

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 $L_\infty$, 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 $L_\infty$ 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 $L_\infty$ of 0.4 and 57, respectively. Note that the values of $L_\infty$ 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).

<table>
<thead>
<tr>
<th>Column</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Rows</td>
<td>AGE</td>
<td>$L_{obs}$</td>
<td>$L_{pre}$</td>
<td>$(L_{obs} - L_{pre})^2$</td>
<td></td>
</tr>
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<td>2</td>
<td>1</td>
<td>25</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>2</td>
<td>36</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>3</td>
<td>42</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>4</td>
<td>47</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>5</td>
<td>51</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
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<td>6</td>
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<td>-</td>
<td>-</td>
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</tr>
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<td>8</td>
<td>7</td>
<td>54</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>SUM(D2:D8)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>11</td>
<td>K =</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>$L_\infty$ =</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>13</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>14</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Another growth curve that is sometimes used to describe the increase in fish weight with age is the Gompertz function (Ricker 1979):

\[ W_t = W_0 e^{\left[G \left(1-e^{-g_t}\right)\right]} \]

where \(W_t\) is weight at time \(t\),
- \(t\) is the age of fish,
- \(W_0\) is a hypothetical weight at \(t = 0\),
- \(G\) is an instantaneous growth parameter when \(t = 0\), and
- \(g\) is the instantaneous rate of decrease of the instantaneous rate of growth (\(G\)).

The Gompertz function has a sigmoid shape with an upper asymptote of \(W_0 e^x\) at \(t = \infty\) and a lower asymptote of \(W = 0\) at \(t = -\infty\). The inflection point is \(\frac{1}{e} \left(W_0\right)\).

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 (\(W_0\), \(G\), and \(g\)), requiring non-linear estimation techniques for large data sets.
Exercises

1. Given the following age-length data set for mackerel, determine \( K, L_\infty, \) and \( t_0 \) using Ford-Walford and non-linear methods.

<table>
<thead>
<tr>
<th>Age</th>
<th>Length</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>15.1</td>
</tr>
<tr>
<td>2</td>
<td>22.7</td>
</tr>
<tr>
<td>3</td>
<td>27.5</td>
</tr>
<tr>
<td>4</td>
<td>32.3</td>
</tr>
<tr>
<td>5</td>
<td>34.8</td>
</tr>
<tr>
<td>6</td>
<td>37.1</td>
</tr>
</tbody>
</table>

2. Given the following lengths at age for herring, determine \( K, L_\infty, \) and \( t \) using Gulland-Holt and non-linear methods.

<table>
<thead>
<tr>
<th>Age</th>
<th>Length</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>25.7</td>
</tr>
<tr>
<td>4</td>
<td>28.4</td>
</tr>
<tr>
<td>5</td>
<td>30.2</td>
</tr>
<tr>
<td>6</td>
<td>31.7</td>
</tr>
<tr>
<td>7</td>
<td>32.8</td>
</tr>
<tr>
<td>8</td>
<td>33.7</td>
</tr>
<tr>
<td>9</td>
<td>34.4</td>
</tr>
<tr>
<td>10</td>
<td>34.9</td>
</tr>
<tr>
<td>11</td>
<td>35.6</td>
</tr>
<tr>
<td>12</td>
<td>36.0</td>
</tr>
<tr>
<td>13</td>
<td>35.9</td>
</tr>
<tr>
<td>14</td>
<td>37.0</td>
</tr>
<tr>
<td>15</td>
<td>37.7</td>
</tr>
</tbody>
</table>
Bibliography


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 ($R$) into the stock and growth ($G$) 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.

\[
\text{Stock Size} = (R + G) - (M + F)
\]

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 instantaneous rate is a constant as the slope of the relationship between the rate of loss $\left(\frac{dN}{dt}\right)$ and population size ($N$) is a straight line (Figure 2).

**Figure 2. Relationship between the rate of loss $\left(\frac{dN}{dt}\right)$ and population size ($N$).**

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 or decay equation because it describes the decline in numbers over time. The parameter \( N_0 \) is the number of animals in the population at time 0 and \( N_t \) is the number present at time \( t \). The parameter \( Z \) is the total instantaneous mortality rate. Figure 3 shows the relationship between \( N_t \) and time for various levels of mortality and for \( N_0 = 1000 \) individuals.

The decay equation can also be expressed as:

\[ N_t = N_{t-1} e^{-Z} \]

where \( t \) is assumed to be equal to 1, and \( N_{t-1} \) is the population size in the previous year.
Figure 3. Exponential decay curves for $Z = 0.2$, $0.5$, $1.0$, and $2.0$ with recruitment $N_0 = 1000$ fish.

At low values (0.2) of $Z$, a cohort of animals reduces to an effective zero number (5% of their initial number) in about 20 years. At moderate values (0.5) of $Z$, a cohort of animals reduces to an effective zero number in about 8 years. At high values (1.0 and greater) of $Z$, a cohort of animals reduces to an effective zero number in 1-2 years.

The annual survival proportion ($S$) is the ratio of the number at the end of time $t$ divided by the number at the start of time $t$:

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

Solving for $Z$ gives:

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

Example 1: If the instantaneous 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 365 days (i.e., the “instant” time is one day), then $2/365$ or 0.548% of the population will die each day. On the first day of the year, 5,480 fish will die ($1,000,000 \times 0.00548$), leaving 994,520 alive. Similarly, 5,450 fish will die on the second day. If $\rho$ is the proportion of fish that dies every day, then $q = 1-\rho$ is the proportion of fish that survives. Table 1 describes the decrease in numbers over time.

At the end of the year, $[1,000,000 \times (1-0.00548)^{365}] = 134,566$ fish remain alive = $N_t$.

<table>
<thead>
<tr>
<th>Time</th>
<th>Number of fish dead</th>
<th>Number surviving</th>
</tr>
</thead>
<tbody>
<tr>
<td>1st day</td>
<td>$pN_0$</td>
<td>$qN_0$</td>
</tr>
<tr>
<td>2nd day</td>
<td>$p?qN_0$</td>
<td>$q^2N_0$</td>
</tr>
<tr>
<td>3rd day</td>
<td>$p?q^2N_0$</td>
<td>$q^3N_0$</td>
</tr>
<tr>
<td>............</td>
<td>..........</td>
<td>..........</td>
</tr>
<tr>
<td>n$^{th}$ day</td>
<td>$p?q^{n-1}N_0$</td>
<td>$q^nN_0$</td>
</tr>
</tbody>
</table>

If we had instead selected a smaller ‘instant’ of time, say 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 135,673 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 survival equation mentioned above, or, in this example:

$$ N_t = N_0 e^{-2} = 1,000,000 \times e^{-2} = 135,335 \text{ fish}. $$
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.

For both Type 1 and Type 2 fisheries, the natural and fishing mortality rates must be accounted for to determine the 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 proportioned instantaneous mortality rates separately. Under the scenario shown in Figure 4, 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. For Type 2 fisheries, 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 zero, then natural mortality is the sole cause of cohort number decline. The natural mortality rate is directly related to the life span of the species (Table 2). Long-lived species, with life spans of 15 years or more, have relatively low natural mortality rates ($M \leq 0.2$). Short-lived species, with life spans of 5 years or less, have relatively high natural mortality rates ($M \geq 0.7$).
Table 2. Relationship between instantaneous natural mortality, annual percent loss, and life span.

<table>
<thead>
<tr>
<th>Instantaneous Mortality</th>
<th>Annual Percent Loss</th>
<th>Life Span</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.05</td>
<td>5</td>
<td>60</td>
</tr>
<tr>
<td>0.10</td>
<td>10</td>
<td>30</td>
</tr>
<tr>
<td>0.20</td>
<td>18</td>
<td>15</td>
</tr>
<tr>
<td>0.50</td>
<td>40</td>
<td>6</td>
</tr>
<tr>
<td>0.70</td>
<td>50</td>
<td>5</td>
</tr>
<tr>
<td>1.00</td>
<td>64</td>
<td>3</td>
</tr>
<tr>
<td>1.50</td>
<td>78</td>
<td>2</td>
</tr>
</tbody>
</table>

Example 2: Consider a fish stock with a five year life span where $M = 0.7$. Develop a trajectory of cohort number as a function of age, starting with 1000 individuals.

Solution: If $M = 0.7$, then $S = e^{-Z} = e^{-0.7} = 0.50 = 50\%$

<table>
<thead>
<tr>
<th>Age</th>
<th>Cohort Number</th>
<th>Percent Annual Mortality</th>
<th>Percent Annual Survival</th>
<th>Percent Remaining</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>1000</td>
<td>50</td>
<td>50</td>
<td>100</td>
</tr>
<tr>
<td>1</td>
<td>500</td>
<td>50</td>
<td>50</td>
<td>50</td>
</tr>
<tr>
<td>2</td>
<td>250</td>
<td>50</td>
<td>50</td>
<td>25</td>
</tr>
<tr>
<td>3</td>
<td>125</td>
<td>50</td>
<td>50</td>
<td>12</td>
</tr>
<tr>
<td>4</td>
<td>63</td>
<td>50</td>
<td>50</td>
<td>6</td>
</tr>
<tr>
<td>5</td>
<td>31</td>
<td>50</td>
<td>50</td>
<td>3</td>
</tr>
</tbody>
</table>

The proportion of annual mortality due to fishing can also be expressed as an annual rate of exploitation, which is defined as the annual percent removal rate ($U$). Exploitation rate is also defined as the proportion of the population harvested annually ($U = \text{Catch} / \text{initial population size}$).

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

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

In a Type 2 fishery, the exploitation rate is calculated as
Fishing mortality is generally not applied over the life span of a cohort, but is initiated when the fish recruit to the fishery ($t_c$) based on age, size, or geographic relocation. When fishing mortality is added to natural mortality, the rate of decline in cohort number is accelerated (Figure 6).

**Figure 6.** Exponential decay of cohort number when $M = 0.2$ and $F = 1.0$ applied at $t_c$, age 3.

**Example 3:** Consider a cohort 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. Assume Type 2 fishery.

**Solution:**

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

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

$$
U = \frac{C}{N_0} = \frac{321}{1000} = 0.321
$$

$$
F = \frac{(U * Z)}{\left(1 - e^{-Z}\right)} = \frac{(0.321 * 1.027)}{\left(1 - e^{-1.027}\right)} = 0.329 = 0.514
$$

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

See answers to examples for clarification.
**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 logarithm 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 based on 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 is linearized, the slope, a straight line, is the total mortality rate (Figure 7).

![Figure 7. The linearized exponential decay function: $\ln N_t = Zt + b$](image)

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

$$\ln(C_t) = Zt + b$$

where $t$ is time in years. The assumption is that total catch or CPUE is a proxy for abundance of the cohort at specific age.

The absolute value of the slope 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.

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.

<table>
<thead>
<tr>
<th>Age</th>
<th>Numbers</th>
<th>Ln(Ct)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.5</td>
<td>-0.69</td>
</tr>
<tr>
<td>2</td>
<td>98</td>
<td>4.59</td>
</tr>
<tr>
<td>3</td>
<td>658</td>
<td>6.48</td>
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<td>4</td>
<td>664</td>
<td>6.49</td>
</tr>
<tr>
<td>5</td>
<td>551</td>
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<td>6</td>
<td>476</td>
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<td>7</td>
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<td>8</td>
<td>216</td>
<td>5.37</td>
</tr>
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<td>143</td>
<td>4.90</td>
</tr>
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<td>10</td>
<td>44</td>
<td>4.26</td>
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<tr>
<td>11</td>
<td>48</td>
<td>3.77</td>
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<td>12</td>
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<td>13</td>
<td>4.6</td>
<td>2.58</td>
</tr>
<tr>
<td>14</td>
<td>2.6</td>
<td>1.52</td>
</tr>
<tr>
<td>15+</td>
<td>0.95</td>
<td></td>
</tr>
</tbody>
</table>

Figures 8 and 9 show 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 8.** Catch curve analysis.  
**Figure 9.** Observed and predicted population size.

Catch curves are very simple to calculate, but they hide numerous assumptions that one has to consider when interpreting 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 also 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 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:

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

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

$$\text{Var}(\hat{N}) = \frac{C_1^2 C_2 (C_2 - R)}{R^2} \quad \text{and} \quad \text{Var}(U) = \frac{R(C_2 - R)}{C_1^2 C_2}.$$ 

The exploitation rate is converted to an instantaneous rate using either

$$U = 1 - e^{-Z}$$

for a Type 1 fishery, or

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

for a Type 2 fishery. 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 5: 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:

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

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 $M = 0.15$. 

IV - 11
<table>
<thead>
<tr>
<th>Year</th>
<th>Tagged</th>
<th>Recaptured</th>
<th>Rate of Exploitation</th>
</tr>
</thead>
<tbody>
<tr>
<td>1986</td>
<td>5797</td>
<td>1194</td>
<td>0.21</td>
</tr>
<tr>
<td>1987</td>
<td>5680</td>
<td>1356</td>
<td>0.24</td>
</tr>
<tr>
<td>1988</td>
<td>6836</td>
<td>1727</td>
<td>0.25</td>
</tr>
<tr>
<td>1989</td>
<td>6436</td>
<td>1235</td>
<td>0.19</td>
</tr>
<tr>
<td>1990</td>
<td>5741</td>
<td>1066</td>
<td>0.19</td>
</tr>
<tr>
<td>1991</td>
<td>6136</td>
<td>1109</td>
<td>0.18</td>
</tr>
<tr>
<td>1992</td>
<td>9126</td>
<td>1842</td>
<td>0.20</td>
</tr>
<tr>
<td>1993</td>
<td>8177</td>
<td>1708</td>
<td>0.21</td>
</tr>
<tr>
<td>1994</td>
<td>7533</td>
<td>1974</td>
<td>0.26</td>
</tr>
<tr>
<td>1995</td>
<td>5307</td>
<td>963</td>
<td>0.18</td>
</tr>
<tr>
<td>1996</td>
<td>6221</td>
<td>997</td>
<td>0.16</td>
</tr>
<tr>
<td>1997</td>
<td>6102</td>
<td>1665</td>
<td>0.27</td>
</tr>
</tbody>
</table>

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:

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

Substituting for $N_r$ yields

$$n_r = \left[ \frac{F}{(F+M)} \right] \left[ N_0 \left[ e^{-(F+M)T} \right] \left[ 1 - e^{-(F+M)T} \right] \right].$$
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 6:** 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 mortality ($Z$) and fishing mortality ($F$) over the time period, assuming a natural mortality rate of $M = 0.30$.

<table>
<thead>
<tr>
<th>Year</th>
<th>$n_r$</th>
<th>$\ln(n_r)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1991</td>
<td>270</td>
<td>5.6</td>
</tr>
<tr>
<td>1992</td>
<td>36</td>
<td>3.6</td>
</tr>
<tr>
<td>1993</td>
<td>6</td>
<td>1.8</td>
</tr>
<tr>
<td>1994</td>
<td>1</td>
<td>0</td>
</tr>
</tbody>
</table>

Conducting a linear regression of $\ln(n_r)$ as a function of time in years (Figure 10) 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.
These types of estimates hold assumptions of equal survivorship, complete reporting, and no tag loss or tag mortality. In the real world, these assumptions 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.

**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 11). 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 11. Plot of $Z = qf + M$. In this example, $q = 0.0013$ and $M = 0.2118$.

**Example 7:** 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 12. The $y$-intercept estimate from the least squares regression equation gives an estimate of $M = 2.05$

<table>
<thead>
<tr>
<th>Year</th>
<th>Year Effort ($f$) (x1000 days)</th>
<th>$Z$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1966</td>
<td>2.08</td>
<td>2.41</td>
</tr>
<tr>
<td>1967</td>
<td>2.08</td>
<td>2.69</td>
</tr>
<tr>
<td>1968</td>
<td>3.50</td>
<td>2.72</td>
</tr>
<tr>
<td>1969</td>
<td>3.60</td>
<td>2.62</td>
</tr>
<tr>
<td>1970</td>
<td>3.80</td>
<td>3.73</td>
</tr>
<tr>
<td>1971</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>1972</td>
<td>7.19</td>
<td>3.68</td>
</tr>
<tr>
<td>1973</td>
<td>9.94</td>
<td>4.61</td>
</tr>
<tr>
<td>1974</td>
<td>6.06</td>
<td>3.30</td>
</tr>
</tbody>
</table>

Figure 12. Linear regression of $Z$ against $f$ to solve for $M$.

**Other Methods for Estimating Natural Mortality**

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

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

where $T_{\text{max}}$ is the maximum age or longevity.

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 3 shows values of $M$ for several species based on Hoenig’s $3/T_{\text{max}}$ 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>
<thead>
<tr>
<th>Species</th>
<th>Longevity (years)</th>
<th>$M$ (Hoenig 1983)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Croaker</td>
<td>5</td>
<td>0.60</td>
</tr>
<tr>
<td>Menhaden</td>
<td>8</td>
<td>0.375</td>
</tr>
<tr>
<td>Bluefish</td>
<td>8</td>
<td>0.375</td>
</tr>
<tr>
<td>Cod</td>
<td>20</td>
<td>0.15</td>
</tr>
<tr>
<td>Striped bass</td>
<td>30</td>
<td>0.10</td>
</tr>
<tr>
<td>Tautog</td>
<td>30</td>
<td>0.10</td>
</tr>
<tr>
<td>Red Drum</td>
<td>50</td>
<td>0.06</td>
</tr>
<tr>
<td>Atlantic Sturgeon</td>
<td>60</td>
<td>0.05</td>
</tr>
</tbody>
</table>
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 $N_b$, $U$, $Z$, $F$ 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.

2. 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 $M = 0.25$.

<table>
<thead>
<tr>
<th>Year</th>
<th>Age 1</th>
<th>Age 2</th>
<th>Age 3</th>
<th>Age 4</th>
<th>Age 5</th>
</tr>
</thead>
<tbody>
<tr>
<td>1985</td>
<td>10.39</td>
<td>4.12</td>
<td>0.93</td>
<td>0.06</td>
<td>0.03</td>
</tr>
<tr>
<td>1990</td>
<td>3.45</td>
<td>0.73</td>
<td>0.13</td>
<td>0.06</td>
<td>0.019</td>
</tr>
</tbody>
</table>

   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 cohorts or year classes 1990, 1993, and 1996. Natural mortality for striped bass is $M = 0.15$.

<table>
<thead>
<tr>
<th>Year of release (year classes)</th>
<th>Number released</th>
<th>Recaptures</th>
</tr>
</thead>
<tbody>
<tr>
<td>1988</td>
<td>227</td>
<td>1988</td>
</tr>
<tr>
<td>1989</td>
<td>387</td>
<td>1989</td>
</tr>
<tr>
<td>1990</td>
<td>446</td>
<td>1990</td>
</tr>
<tr>
<td>1991</td>
<td>537</td>
<td>1991</td>
</tr>
<tr>
<td>1992</td>
<td>699</td>
<td>1992</td>
</tr>
<tr>
<td>1993</td>
<td>381</td>
<td>1993</td>
</tr>
<tr>
<td>1994</td>
<td>462</td>
<td>1994</td>
</tr>
<tr>
<td>1995</td>
<td>683</td>
<td>1995</td>
</tr>
</tbody>
</table>

Bibliography


SELECTIVITY OF MARINE FISH HARVESTING GEARS:
GENERAL THEORY, SIZE SELECTION EXPERIMENTS AND
DETERMINATION OF SIZE SELECTION CURVES

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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 \( L_1 \) and larger than another particular size \( L_2 \) are not captured, and that fish of a certain size \( L_{\text{opt}} \) between \( L_1 \) 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 and 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 a 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 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 codend meshes and some hooks can be represented by a logistic cumulative distribution function (LCDF) (Figure 1) of the form:

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

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

$$PL_L = \left(1 + e^{-(\alpha 2 + \beta L)}\right)^{-1}$$

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

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

The terms $\alpha$ and $\beta$ 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:

$$\ln(P/(1 - P)) = \alpha + (\beta * L).$$
The LCDF curve is unique for a particular fish species, mesh size, and mesh shape. The selection factor \((SF)\) is defined as:

\[
SF = \frac{L_{50}}{ml}
\]

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).
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):

\[
PN_L = e^{\left(\frac{-(L-L_{opt})}{2 \times SD^2}\right)}
\]

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 of the 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.
The values of $L_{opt}$ 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 $ml_B$:

$$L_{optA} = -2*[(a*ml_A) / (b*(ml_A + ml_B))]$$

$$L_{optB} = -2*[(a*ml_B) / b*(ml_A + ml_B))]$$

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

The selection factor $SF$ is:

$$SF = \frac{L_{opt}}{ml}$$

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 codend mesh experiment, the comparative trials are conducted using:

1. A covered codend, where the catch retained in the codend is compared to the catch of the cover and the codend.

2. A trouser trawl with two codends, small mesh and experimental, where the catch retained in the experimental codend is compared to the catch retained in the small mesh codend.

3. Alternate paired tows aboard a single or paired vessels where the catches of the small mesh codends are compared to the catches of the large mesh codends.

Example 1: Covered codend experiment for an idealized roundfish.

The catches by length (cm) for a mesh cover and an experimental codend (12 cm, diamond mesh) are shown below. Solve for \(L_{50}\), selection factor, selection range, and the parameters \(\alpha\) and \(\beta\) that define the LCDF.

<table>
<thead>
<tr>
<th>(L) (cm)</th>
<th>Cover</th>
<th>Codend</th>
<th>Sum</th>
<th>Ratio ((P))</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>10</td>
<td>0</td>
<td>10</td>
<td>0.00</td>
</tr>
<tr>
<td>20</td>
<td>19</td>
<td>1</td>
<td>20</td>
<td>0.05</td>
</tr>
<tr>
<td>30</td>
<td>75</td>
<td>25</td>
<td>100</td>
<td>0.25</td>
</tr>
<tr>
<td>40</td>
<td>200</td>
<td>200</td>
<td>400</td>
<td>0.50</td>
</tr>
<tr>
<td>50</td>
<td>100</td>
<td>300</td>
<td>400</td>
<td>0.75</td>
</tr>
<tr>
<td>60</td>
<td>2</td>
<td>198</td>
<td>200</td>
<td>0.99</td>
</tr>
<tr>
<td>70</td>
<td>0</td>
<td>50</td>
<td>50</td>
<td>1.00</td>
</tr>
<tr>
<td>80</td>
<td>0</td>
<td>5</td>
<td>5</td>
<td>1.00</td>
</tr>
</tbody>
</table>

The selection curve is plotted, and graphically the \(L_{50}\) is estimated to be 40 cm. In addition, graphically, the \(L_{75}\) and \(L_{25}\) are estimated to be 50 and 30 cm, respectively.

The selection factor is \(40 \text{ cm}/12 \text{ cm} = 3.3\)

The selection range is \(L_{75}-L_{25} = 20 \text{ cm}\)

The parameters \((\alpha\) and \(\beta\)) defining the LCDF are determined indirectly using linear regression on the transformed equation or directly using non-linear regression. These results are illustrated in Table 1 and Figure 7.
Table 1. Results of the covered codend experiment.

<table>
<thead>
<tr>
<th>$L$ (cm)</th>
<th>Cover</th>
<th>Codend</th>
<th>Sum</th>
<th>Ratio ($P$)</th>
<th>$\ln \left( \frac{P}{1-P} \right)$</th>
<th>Predicted $P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>10</td>
<td>0</td>
<td>10</td>
<td>0.00</td>
<td>0.008</td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>19</td>
<td>1</td>
<td>20</td>
<td>0.05</td>
<td>-2.94</td>
<td>0.042</td>
</tr>
<tr>
<td>30</td>
<td>75</td>
<td>25</td>
<td>100</td>
<td>0.25</td>
<td>-1.10</td>
<td>0.198</td>
</tr>
<tr>
<td>40</td>
<td>200</td>
<td>200</td>
<td>400</td>
<td>0.50</td>
<td>0.00</td>
<td>0.582</td>
</tr>
<tr>
<td>50</td>
<td>100</td>
<td>300</td>
<td>400</td>
<td>0.75</td>
<td>1.10</td>
<td>0.887</td>
</tr>
<tr>
<td>60</td>
<td>2</td>
<td>198</td>
<td>200</td>
<td>0.99</td>
<td>4.60</td>
<td>0.978</td>
</tr>
<tr>
<td>70</td>
<td>0</td>
<td>50</td>
<td>50</td>
<td>1.00</td>
<td>0.996</td>
<td></td>
</tr>
<tr>
<td>80</td>
<td>0</td>
<td>5</td>
<td>5</td>
<td>1.00</td>
<td>0.999</td>
<td></td>
</tr>
</tbody>
</table>

![Graph showing the relationship between length and probability](image-url)
Figure 7. Results of the covered codend 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 below. 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.

<table>
<thead>
<tr>
<th>Length</th>
<th>( A )</th>
<th>( B )</th>
<th>( \ln(B/A) )</th>
</tr>
</thead>
<tbody>
<tr>
<td>18</td>
<td>20</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>19</td>
<td>90</td>
<td>1</td>
<td>-4.5</td>
</tr>
<tr>
<td>20</td>
<td>199</td>
<td>9</td>
<td>-3.1</td>
</tr>
<tr>
<td>21</td>
<td>182</td>
<td>53</td>
<td>-1.2</td>
</tr>
<tr>
<td>22</td>
<td>119</td>
<td>290</td>
<td>-0.9</td>
</tr>
<tr>
<td>23</td>
<td>29</td>
<td>357</td>
<td>2.5</td>
</tr>
<tr>
<td>24</td>
<td>4</td>
<td>225</td>
<td>4.0</td>
</tr>
<tr>
<td>25</td>
<td>0</td>
<td>101</td>
<td>-</td>
</tr>
</tbody>
</table>

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.
Figure 8. Analysis and results of NPDF selectivity analysis.
Exercises

**TRAWL CODEND SELECTION PROBLEM**

**COVERED CODEND EXPERIMENT**

Yellowtail flounder on Georges Bank

Codend = 14 cm, diamond mesh; Cover = 5 cm, square mesh

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

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 codend.
TRAWL CODEND SELECTION PROBLEM

ALTERNATE TOW EXPERIMENT

Cod on Georges Bank

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

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

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 codend.
**GILLNET SELECTION PROBLEM FOR COD**

<table>
<thead>
<tr>
<th>Fish Length (cm)</th>
<th>Webbing A 13.6 cm</th>
<th>Webbing B 14.8 cm</th>
<th>Webbing C 16.0 cm</th>
</tr>
</thead>
<tbody>
<tr>
<td>46</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>48</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>50</td>
<td>26</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>52</td>
<td>52</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>54</td>
<td>102</td>
<td>16</td>
<td>4</td>
</tr>
<tr>
<td>56</td>
<td>295</td>
<td>131</td>
<td>17</td>
</tr>
<tr>
<td>58</td>
<td>309</td>
<td>362</td>
<td>95</td>
</tr>
<tr>
<td>60</td>
<td>118</td>
<td>326</td>
<td>199</td>
</tr>
<tr>
<td>62</td>
<td>79</td>
<td>191</td>
<td>202</td>
</tr>
<tr>
<td>64</td>
<td>27</td>
<td>111</td>
<td>133</td>
</tr>
<tr>
<td>66</td>
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<td>44</td>
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<td>8</td>
<td>14</td>
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<td>8</td>
<td>15</td>
</tr>
<tr>
<td>72</td>
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<td>1</td>
<td>5</td>
</tr>
<tr>
<td>74</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>76</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

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.


Otway, N. M. and J. A. Craig. 1993. Effects of hook size on the catches of undersized snapper


Background

Models of yield per recruit (YPR) and spawning stock biomass per recruit (SPR or SSBPR) used in the analysis of fish population dynamics have sometimes assumed knife-edge selection at a single length or age. The purpose of this chapter is to review the analytical solution to the YPR model assuming knife-edge selection, and to integrate gear-specific size selection into YPR and SPR discrete time models. The development of a generalized model applied to a hypothetical or "idealized" roundfish is the 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.

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).

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
\[ W_\infty \] 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 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:

\[
dC_t = F_t \ast N_t \ast dt
\]

and

\[
dY_t = F_t \ast N_t \ast W_t dt
\]

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:

\[
F_t = 0 \quad \text{and} \quad t < t_c
\]

\[
F_t = F = \text{constant} \quad \text{for} \quad t \geq t_c
\]

\[
Z_t = M \quad \text{for} \quad t < t_c
\]

\[
Z_t = F + M \quad \text{for} \quad t \geq t_c
\]

\[
N_t = R e^{-M(t-t_c)} \quad \text{for} \quad t < t_c
\]

where \( Z_t \) is the total mortality coefficient, and
\( R \) is the total number of recruits in the cohort.

Therefore,

\[
N_t = R' e^{-M(t-t_c)} \quad \text{for} \quad t \geq t_c
\]

where \( R' \) is the number of fish recruiting to the fishery at time \( t = t_c \), and therefore,
\[ R' = R \ e^{-Mt_c}. \]

Thus the total number caught is:

\[
C = \int_{t_c}^{t_L} R' * F e^{-(F+M)(t-t_c)} \ dt
= R'(F/(F+M))\left(e^{-M(t_c)}\right)\left(1 - e^{M(t_L-t_c)}\right)
\]

or

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

and ignoring the last term if \( t_L >> t_c \)

\[
C = (F/(F+M))R'.
\]

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

\[ W_t = W_\infty \left[1 - e^{(-Kt)}\right]^n. \]

This equation is expanded to:

\[ W_t = W_\infty \sum_{n=0}^{3} U_n e^{(-nKt)} \]

where \( U_0 = 1, U_1 = -3, U_2 = 3, U_3 = -1. \)

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

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

Yield per recruit is obtained by normalizing the total yield by the number of recruits \( R' \) in the cohort.
Beverton and Holt (1957) 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 ($M/K \leq 0.5$), 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 only light fishing mortality on smaller fish.

If $M/K$ is large ($M/K \geq 2.0$), 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:

$$Y = Y' \left[ R * W * e^{(-M/l_c)} \right]$$

where

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

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. (Instructions for creating similar tables can be found on the “Answers to Exercises” disk in the file “Chapter 6 – Tables 1&2.xls.”)
<table>
<thead>
<tr>
<th>Rate of Exploitation</th>
<th>Yield per recruit for $M/K = 0.5$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$L_r /x_r$</td>
<td></td>
</tr>
<tr>
<td>0.98</td>
<td>0.060627, 0.013843, 0.020748</td>
</tr>
<tr>
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<td>0.095956, 0.019168, 0.028699</td>
</tr>
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<td>0.101154, 0.022987, 0.034382</td>
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<td>0.91</td>
<td>0.10327, 0.025976, 0.038837</td>
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<td>0.104172, 0.028436, 0.042479</td>
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<td>0.105322, 0.030503, 0.045529</td>
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</tr>
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<td>0.202470, 0.042923, 0.060386</td>
</tr>
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<td>0.202496, 0.042853, 0.060050</td>
</tr>
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<td>0.202517, 0.042787, 0.059652</td>
</tr>
<tr>
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<td>0.202536, 0.042715, 0.059276</td>
</tr>
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<td>0.202552, 0.042643, 0.058919</td>
</tr>
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<td>0.10</td>
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</tr>
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</tr>
<tr>
<td>0.01</td>
<td>0.202612, 0.042219, 0.057185</td>
</tr>
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</table>

Table 1. Yield per recruit for $M/K = 0.5$.
\[
E = \frac{(F/M)}{L}
\]

<table>
<thead>
<tr>
<th>(L/L_o)</th>
<th>0.98</th>
<th>0.96</th>
<th>0.94</th>
<th>0.92</th>
<th>0.88</th>
<th>0.82</th>
<th>0.75</th>
<th>0.70</th>
<th>0.62</th>
<th>0.46</th>
<th>0.40</th>
<th>0.24</th>
<th>0.20</th>
<th>0.14</th>
<th>0.12</th>
</tr>
</thead>
<tbody>
<tr>
<td>(F/F_{o})</td>
<td>0.000019</td>
<td>0.000074</td>
<td>0.000159</td>
<td>0.000271</td>
<td>0.000406</td>
<td>0.000560</td>
<td>0.000729</td>
<td>0.000912</td>
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<td>0.000000</td>
<td>0.000000</td>
<td>0.000000</td>
<td>0.000000</td>
<td></td>
</tr>
</tbody>
</table>

| 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 |
| 0.000038 | 0.000038 | 0.000038 | 0.000038 | 0.000038 | 0.000038 | 0.000038 | 0.000038 | 0.000038 | 0.000038 | 0.000038 | 0.000038 | 0.000038 | 0.000038 | 0.000038 | 0.000038 | 0.000038 | 0.000038 |

**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 ($F_{\text{MAX}}$)?

The result of those calculations are illustrated as Figure 1. At a $t_c = 3$, the maximum yield per recruit is 1.67 kg at $F = 0.19$. In contrast if the $t_c = 5$, the maximum yield per recruit is 2.02 kg at an $F = 0.31$, an increase of 21%.

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.

![Figure 1](image.png)

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

(A) $t_c = 3.0$

(B) $t_c = 5.0$. 

<table>
<thead>
<tr>
<th></th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$M$</td>
<td>0.1</td>
</tr>
<tr>
<td>$W_\infty$</td>
<td>10</td>
</tr>
<tr>
<td>$K$</td>
<td>0.2</td>
</tr>
<tr>
<td>$t_0$</td>
<td>0</td>
</tr>
<tr>
<td>$t_c$</td>
<td>3</td>
</tr>
<tr>
<td>$t_r$</td>
<td>0</td>
</tr>
<tr>
<td>$N_{tr}$</td>
<td>100000</td>
</tr>
<tr>
<td>$t_y$</td>
<td>20</td>
</tr>
<tr>
<td>$M/K$</td>
<td>0.50</td>
</tr>
</tbody>
</table>
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 $L_\infty$ 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:

$$W_t = (aL_t)^b$$

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:

$$P_t = \left(1 + e^{(-\alpha_1 \cdot (t - \beta_1))}\right)^{-1}$$

where $\alpha_1$ is the steepness of the curve, and $\beta_1$ 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:

$$N_t = N_{(t-i)} e^{(-M)}$$

where $M$ is the instantaneous natural mortality, 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:

$$B_t = N_t \cdot W_t$$

and the unfished spawning stock biomass (UFSSB) of the individuals remaining in the cohort at age $t$ is determined:
Based on gear selection literature, trawls and hooks are assumed to possess qualitatively similar size-selection characteristics, which can be represented by a LCDF of individual fish length ($PL_t$):

$$PL_t = \left(1 + e^{-\alpha (L - L_{50})} \right)^{-1}$$

where $\alpha$ = 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 ($PN_t$):

$$PN_t = \left[1 - \left(1 - e^{-\alpha (L - L_{opt})} \right)^{-1} \right] \left(1 - e^{-\alpha (L - L_{50})} \right)^{-1}$$

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

Applying length-specific susceptibility to fishing ($PN_t$ or $PLL_t$) 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:

$$NF_t = NF_{t-1} - \frac{(PN_t \ or \ PLL_t) \times F}{(PN_t \ or \ PLL_t) + M} \times NF_{t-1} \times (W)$$

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

$$Y_t = \left[\left(\frac{PN_t \ or \ PLL_t F}{(PN_t \ or \ PLL_t F + M)} \times NF_t \times (W)\right)\right]$$

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

$$SSB_t = (NF_t \times (W)) \times F$$

Given these equations and specific values of $L_{\infty}$, $K$, $a$, $b$, and $M$, the total biomass and spawning stock biomass of the unfished cohort are determined. By evaluating a wide range of $L_{\infty}$, $L_{opt}$, and $F$ values, the resulting matrix of data, expressed as percentage of the maximum value, is contoured to produce isopleth diagrams of yield per recruit (YPR) and spawning stock biomass per recruit (SSB).
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: \( L_\infty = 100 \text{ cm} \), \( W_\infty = 10 \text{ kg} \), \( K = 0.2 \), \( a = 0.00001 \), \( b = 3 \), \( \alpha = 1 \), \( \beta = 3 \), and \( M = 0.2 \).

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, and 
(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, and 
(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 $L_{50S}$ from 50-100 cm and (B) Normal probability density function (NPDF) selectivity curves for $L_{optS}$ 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 $F = 3.0$.  

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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 $F = 3.0$. 
Northwest Atlantic groundfish species have markedly different growth and mortality rates as indicated in the following table.

<table>
<thead>
<tr>
<th>Species</th>
<th>$K$</th>
<th>$M$</th>
<th>$M/K$</th>
<th>$W_{\infty}$</th>
<th>$L_{\infty}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>cod</td>
<td>0.12</td>
<td>0.2</td>
<td>1.7</td>
<td>33.7</td>
<td>148</td>
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<tr>
<td>haddock</td>
<td>0.38</td>
<td>0.2</td>
<td>0.5</td>
<td>4.4</td>
<td>74</td>
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<tr>
<td>silver hake</td>
<td>0.18</td>
<td>0.4</td>
<td>2.2</td>
<td>2.0</td>
<td>65</td>
</tr>
<tr>
<td>winter flounder</td>
<td>0.37</td>
<td>0.2</td>
<td>0.5</td>
<td>3.5</td>
<td>63</td>
</tr>
<tr>
<td>yellowtail flounder</td>
<td>0.63</td>
<td>0.2</td>
<td>0.3</td>
<td>0.9</td>
<td>46</td>
</tr>
<tr>
<td>plaice</td>
<td>0.17</td>
<td>0.2</td>
<td>1.2</td>
<td>2.4</td>
<td>65</td>
</tr>
<tr>
<td>summer flounder</td>
<td>0.21</td>
<td>0.2</td>
<td>1.0</td>
<td>7.6</td>
<td>84</td>
</tr>
</tbody>
</table>

Given this variability in $M/K$ ratios and $L_{\infty}$, 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 $L_t = L_{\infty}(1-e^{-Kt})$.

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 $\alpha = 5$ and $\beta = 2.37$ and length-width relationship parameters are $a = 0.000$ 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.
Bibliography


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 \( (i.e. \text{ these rates are density independent}) \).
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](image_url)

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

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

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

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.

![Image of population trajectories](image)

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

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:
Replacing the initial birth and death rate difference with $\alpha$ and the density dependent birth and death rate coefficients with $\beta$ 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 $N_{\text{MAX}}$, \[ \frac{dN}{dt} = 0 \]

\[N_{\text{MAX}} = \frac{\alpha}{\beta} = \frac{b_0 - d_0}{b_1 + d_1}\]

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:

\[ \frac{d}{dN}[(\alpha - \beta N)N] = 0 \]
\[ \alpha - 2\beta N = 0 \]

\[N = \frac{1}{2}\left(\frac{\alpha}{\beta}\right)\] or $\frac{1}{2}$ carrying capacity.
The differential equation relating $\frac{dN}{dt}$ to $N$ is solved using the separation of variables method:

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

$$N_i = \left[ \frac{\alpha}{\beta} \right] \left[ \frac{1}{((\alpha - \beta N)/\beta N_0)e^{-\alpha t} + 1} \right]$$

substituting

$N_{MAX} = \left( \frac{\alpha}{\beta} \right)$

and

$\gamma = \left( \frac{\alpha - \beta N_0}{\beta N_0} \right)$

yields:

$$N_i = N_{MAX} \left[ 1 + \gamma e^{-\alpha t} \right].$$

Note that this equation has the form of a generalized logistic function (Figure 5).
Anthropogenic mortality or harvesting is added to the model of population regulation as follows:

\[ \frac{dN}{dt} = (\alpha - \beta N)N -aN \]

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:

\[ \text{New Biomass} = \text{Old Biomass} + \text{Recruitment} + \text{Growth} - \text{Catch} - \text{Natural mortality}. \]

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:

\[ \text{New Biomass} = \text{Old Biomass} + \text{Surplus Production} - \text{Catch}. \]
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 \((B)\),

\[
\frac{dB}{dt} = (\alpha - \beta B) - FB.
\]

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

\[
(\alpha - \beta B^*) = F^* \Rightarrow B^* = \frac{(\alpha - F^*)}{\beta}.
\]

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:

\[
\begin{align*}
a & \text{ for } \left( \frac{\alpha}{\beta} \right), \\
b & \text{ for } \left( \frac{1}{\beta} \right), \text{ and} \\
f & \text{ for } F \text{ assuming catchability is constant (based on } F = fq)
\end{align*}
\]

results in the generalized Schaefer Model (1954):
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:

$$
\frac{dY}{df} = a - 2bf = 0
$$

$$
f_{MEY} = \frac{a}{2b}.
$$

MEY is then determined by substituting $f_{MEY}$ back into the original equation:

$$
Y_{MEY} = \left(a - \frac{b}{2b}\right) - b\left(a^2/2b^2\right)
$$

$$
= \frac{a^2}{2b} - \frac{ba^2}{4b^2}
$$

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

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:
\[ \frac{Y}{f} = a - bf, \]

and using linear regression on CPUE \( \left( \frac{Y}{f} \right) \) 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:

\[ f_{\text{MEY}} = \frac{1}{d}, \]
\[ Y_{\text{MEY}} = \left( \frac{1}{d} \right) e^{(c-1)}. \]

**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.
The time history of the catch and effort data is shown in Figure 7.

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.

<table>
<thead>
<tr>
<th>Year</th>
<th>Catch</th>
<th>Effort</th>
</tr>
</thead>
<tbody>
<tr>
<td>1988</td>
<td>50</td>
<td>623</td>
</tr>
<tr>
<td>1989</td>
<td>49</td>
<td>628</td>
</tr>
<tr>
<td>1990</td>
<td>47.5</td>
<td>520</td>
</tr>
<tr>
<td>1991</td>
<td>45</td>
<td>513</td>
</tr>
<tr>
<td>1992</td>
<td>51</td>
<td>661</td>
</tr>
<tr>
<td>1993</td>
<td>56</td>
<td>919</td>
</tr>
<tr>
<td>1994</td>
<td>66</td>
<td>1158</td>
</tr>
<tr>
<td>1995</td>
<td>58</td>
<td>1970</td>
</tr>
<tr>
<td>1996</td>
<td>52</td>
<td>1317</td>
</tr>
</tbody>
</table>

Figure 7. Time history of catch and effort.
<table>
<thead>
<tr>
<th>Year</th>
<th>Catch</th>
<th>Effort</th>
<th>CPUE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1988</td>
<td>50</td>
<td>623</td>
<td>0.080257</td>
</tr>
<tr>
<td>1989</td>
<td>49</td>
<td>628</td>
<td>0.078025</td>
</tr>
<tr>
<td>1990</td>
<td>47.5</td>
<td>520</td>
<td>0.091346</td>
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<td>45</td>
<td>513</td>
<td>0.077156</td>
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<td>51</td>
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<td>0.087719</td>
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<tr>
<td>1993</td>
<td>56</td>
<td>919</td>
<td>0.060936</td>
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<tr>
<td>1994</td>
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<td>1158</td>
<td>0.056995</td>
</tr>
<tr>
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<td>0.029442</td>
</tr>
<tr>
<td>1996</td>
<td>52</td>
<td>1317</td>
<td>0.039484</td>
</tr>
</tbody>
</table>

\[ y = -4 \times 10^{-5} x + 0.1064 \]

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 \( \ln(\text{CPUE}) \) (Table 2), and then linearly regress \( \ln(\text{CPUE}) \) versus effort (Figure 10).

Table 2. Trawl catch and effort data with the \( \ln(\text{CPUE}) \).
<table>
<thead>
<tr>
<th>Year</th>
<th>Catch</th>
<th>Effort</th>
<th>ln(CPUE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1988</td>
<td>50</td>
<td>623</td>
<td>-2.52252</td>
</tr>
<tr>
<td>1989</td>
<td>49</td>
<td>628</td>
<td>-2.55072</td>
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<tr>
<td>1990</td>
<td>47.5</td>
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<td>1995</td>
<td>58</td>
<td>1970</td>
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<tr>
<td>1996</td>
<td>52</td>
<td>1317</td>
<td>-3.23187</td>
</tr>
</tbody>
</table>

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.
Exercises

Given the following catch and effort data for the trawl fishery on this pelagic fish species for the period 1976 to 1995,

<table>
<thead>
<tr>
<th>Year</th>
<th>Catch (10^6 kg)</th>
<th>Effort (10,000 days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1976</td>
<td>104</td>
<td>0.13</td>
</tr>
<tr>
<td>1977</td>
<td>282</td>
<td>0.28</td>
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<tr>
<td>1978</td>
<td>348</td>
<td>0.39</td>
</tr>
<tr>
<td>1979</td>
<td>507</td>
<td>0.51</td>
</tr>
<tr>
<td>1980</td>
<td>548</td>
<td>0.72</td>
</tr>
<tr>
<td>1981</td>
<td>602</td>
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<td>584</td>
<td>1.12</td>
</tr>
<tr>
<td>1983</td>
<td>542</td>
<td>0.96</td>
</tr>
<tr>
<td>1984</td>
<td>487</td>
<td>1.09</td>
</tr>
<tr>
<td>1985</td>
<td>472</td>
<td>1.15</td>
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<td>82</td>
<td>1.58</td>
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<td>75</td>
<td>1.60</td>
</tr>
<tr>
<td>1994</td>
<td>71</td>
<td>1.62</td>
</tr>
</tbody>
</table>

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.
Bibliography


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:

\[ F + M \]

\[ \text{RECRUITS} \quad \text{ADULTS.} \]

\[ \text{RECRUITMENT} \]

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.

$$\frac{dN}{dt} = -(q + pN)N$$

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:
\[ R = 1 / \left( \frac{\alpha + \beta}{S} \right) = \frac{S}{\alpha S + \beta} \]

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.

\[
\frac{dN}{dt} = -(q + pS)N
\]

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 $\alpha$ is the recruits per spawners ($R/S$, the slope) at low stock sizes, and $\beta$ 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 $S_r = \ln(\alpha/\beta)$.

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:

$$R = \frac{\alpha S}{1 + \left(\frac{S}{K}\right)^{\beta}}$$

where $\alpha$ is the slope at the origin, $\beta$ 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 ($\beta$) 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 $\alpha$, $K$, and $\beta$ values.

**Estimation of S-R Parameters**

The general form of Beverton-Holt model can be rearranged as follows:

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

$$S/R = \beta + \alpha S.$$  

In the rearranged form, the Beverton-Holt S-R relationship conforms to the basic linear model:

$$y = ax + b$$

where $y = S/R$

$a =$ slope $= \alpha$

$x =$ $S$

$b =$ intercept $= \beta$. 
The $\alpha$ and $\beta$ 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 $\alpha$ and $\beta$ using both the linear and non-linear methods of the Beverton-Holt model.

<table>
<thead>
<tr>
<th>Year</th>
<th>Stock</th>
<th>Recruitment</th>
<th>$S/R$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>8.8</td>
<td>7.1</td>
<td>1.239</td>
</tr>
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<td>2</td>
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<td>6.4</td>
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</tr>
<tr>
<td>3</td>
<td>4.5</td>
<td>6.4</td>
<td>0.703</td>
</tr>
<tr>
<td>4</td>
<td>13.2</td>
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<tr>
<td>5</td>
<td>14.6</td>
<td>7.7</td>
<td>1.896</td>
</tr>
<tr>
<td>6</td>
<td>7.0</td>
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</tr>
<tr>
<td>7</td>
<td>3.1</td>
<td>5.4</td>
<td>0.574</td>
</tr>
<tr>
<td>8</td>
<td>7.7</td>
<td>6.1</td>
<td>1.262</td>
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<tr>
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<td>10.7</td>
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<tr>
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<td>6.0</td>
<td>1.433</td>
</tr>
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<td>15.4</td>
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<td>2.484</td>
</tr>
<tr>
<td>12</td>
<td>2.0</td>
<td>3.5</td>
<td>0.571</td>
</tr>
</tbody>
</table>

The data are fit to a linear model using a regression of $S/R$ versus $S$ (Figure 4). The values of $\alpha$ and $\beta$ are obtained directly from the slope and $y$-intercept values where $\alpha = a$ and $\beta = b$. Therefore, $\alpha = 0.1319$ and $\beta = 0.1824$. Non-linear 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.](image-url)
The general form of the Ricker model is rearranged as follows:

\begin{align*}
R &= \alpha S e^{-\beta S} \\
\frac{R}{S} &= \alpha e^{-\beta S} \\
\ln \left( \frac{R}{S} \right) &= \ln \alpha - \beta S.
\end{align*}

In the rearranged form, the Ricker S-R relationship conforms to the basic linear model:

\[ y = ax + b \]

where \( y = \ln(R/S) \),
\( a = \) slope = \( \beta \),
\( x = S \),
\( b = \) intercept = \( \ln \alpha \).

The \( \alpha \) and \( \beta \) parameters are estimated by regressing \( \ln(R/S) \) against \( S \). After taking the anti-ln of \( \ln \alpha \), 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 \( \alpha \) and \( \beta \) 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 \( \alpha \) is equal to the inverse ln of the y-intercept, therefore \( \alpha = e^{0.7427} = 2.1016 \). The value of \( \beta \) 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).

\[ y = -0.1071x + 0.7427 \]

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:

\[ R = \frac{\alpha S}{1 + \left(\frac{S}{K}\right)^\beta} \cdot \]

Shepherd suggest values for \( \beta \) 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 \( \alpha \) 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:

\[ K = \frac{S^*}{\left(\frac{\alpha S^*}{R^*}\right)^\beta - 1} \cdot \]

**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.](image-url)
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.

<table>
<thead>
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</thead>
<tbody>
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Introduction

In order to obtain meaningful results from a stock assessment, accurate and precise data should be collected and used in the analysis. The utility of the data used depends to a great extent on the sampling methodology employed to collect the data. Data can be collected using fishery dependent or fishery independent methods. Fishery dependent data are collected from fish caught during commercial or recreational fishing activities. Fisheries independent data are collected during research cruises and other sampling activities that are not influenced by directed fishing effort. Both are necessary to fully understand a fish stock and the effects harvest has on the stock. Fishery dependent sampling gathers information on fishing mortality and biological characteristics of the fish caught by commercial and recreational fisheries. Fisheries independent sampling collects biological information on fish from the entire population and is not subject to biases resulting from changes in fishing regulations or the commercial market.

Sampling Design

It is rarely, if ever, possible to obtain information on every fish in a population. Populations must therefore be sampled, and the results of the sample analysis extrapolated to the entire population or the portion of the population of interest (e.g., a specific size class). The problem is therefore how to obtain a representative sample of fish with respect to time and space.

Before sampling can begin, it is necessary to develop a sampling frame, or sampling scheme, which provides the framework utilized to collect a sample. The sampling frame consists of a complete list of all possible sampling units. Sampling units are the smallest unit of study that meet the following criteria:

- They are randomly selected directly from the entire set of sampling units \((i.e., \text{the sampling frame})\), and
- Each unit is independent of all other sampling units.

Sampling units are made up of elements which are not independent and can not be randomly sampled directly. For example, it is not possible to take a random sample of croaker from the Chesapeake Bay because the location of one croaker may influence the location of others \((i.e., \text{they are not independent})\). It is, however, possible to take a random sample of trawl tows from the Chesapeake Bay to collect croaker. The sampling frame would consist of all possible trawl tows in the Bay. Each trawl tow would be a sampling unit, and the croaker would be elements within the sampling units.
Once the sampling frame is developed, a sampling strategy is chosen. Some sampling strategies that are commonly used are simple random, stratified random, and systematic sampling. The sampling strategy chosen will depend on the objectives of the study and the population of sampling units (i.e., the sampling frame) in question. Any information that is known about a species prior to sampling may be beneficial in determining a sampling strategy. The amount of heterogeneity in the fish population is also helpful in determining the sampling strategy that should be employed because a fish population is almost never uniformly distributed throughout its range.

**Simple Random Sampling**

If nothing is known about the population of sampling units before sampling, or the sampling frame is known to be fairly homogeneous, data should be collected using a simple random sample (SRS) design. In a SRS, a sample of \( a \) observations is taken at random from the sampling frame which consists of \( A \) sampling units. Each sampling unit has an equal probability of being chosen for the sample. The mathematical model used to describe SRS is:

\[
y_i = \bar{y} + e_i
\]

where \( y_i \) is the \( i \)th individual observation, 
\( \bar{y} \) is the mean of all observations, and 
\( e_i \) is a random error term.

In other words, the difference between each observation \( y_i \) and the mean \( \bar{y} \) is attributed to random error alone (\( e_i \)).

The sample mean \( \bar{y} \) is an unbiased estimate of the population mean \( \mu \) and can be found using the following equation:

\[
\bar{y} = \frac{y_1 + y_2 + \ldots + y_a}{a} = \frac{1}{a} \sum_{i=1}^{a} y_i
\]

where \( a \) is the total number of observations in the sample.

Similarly, the sample variance \( s^2 \) is an unbiased estimate of the population variance \( \sigma^2 \) and is estimated without bias using:

\[
s^2 = \frac{\sum_{i=1}^{a} (y_i - \bar{y})^2}{(a - 1)} \quad \text{or} \quad s^2 = \frac{\sum_{i=1}^{a} y_i^2 - \left( \sum_{i=1}^{a} y_i \right)^2}{a - 1}
\]

The standard deviation \( s \) is found by taking the square root of the variance.
An unbiased estimate of the variance of the mean is found using the following equation:

\[
s_{x}^{2} = \left( \frac{s^{2}}{a} \right) \left( 1 - \frac{a}{A} \right)
\]

where \( s_{x}^{2} \) is the variance of the mean,
\( s^{2} \) is the sample variance,
\( a \) is the total number of observations in the sample, and
\( A \) is the total number of observations in the population.

The square root of this value is the standard deviation of the mean, also known as the standard error of the mean.

**Example 1:** The following table contains trawl survey catch per tow data. Calculate the mean catch per tow (in terms of number caught) for the sampled area, assuming a simple random sample of tows was collected from a total of 150 possible stations. Calculate the variance, standard deviation, and standard error of the mean.

<table>
<thead>
<tr>
<th>Tow Number</th>
<th>Catch per tow</th>
<th>Tow Number</th>
<th>Catch per tow</th>
<th>Tow Number</th>
<th>Catch per tow</th>
<th>Tow Number</th>
<th>Catch per tow</th>
<th>Tow Number</th>
<th>Catch per tow</th>
</tr>
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<td>35</td>
<td>20</td>
<td>11</td>
<td>25</td>
<td>3</td>
</tr>
</tbody>
</table>

Avg 10.4
Var 144.1667
Stddev 12.00694

A potential problem with simple random sampling is that it is possible to take an entire sample from one tail of the normal distribution, resulting in an over or underestimate of the mean. The possibility of this decreases as sample size increases. Another problem is that all sources of bias are encompassed in the error variable \( e \). Simple random sampling does not identify sources of variation in the population.

**Stratified Random Sampling**

Stratified sampling is a method used to separate the effects of specific sources of variation from the random error. Stratified sampling is conducted by first dividing the population of sampling units into strata (i.e. subpopulations) and then sampling within each stratum. The population should be divided so that observations within a stratum are similar; that is, strata should be internally homogenous and externally heterogeneous. Stratified sampling is therefore most
effective when the population is known to be non-homogeneous. If SRS is used to sample within the strata, this methodology is termed stratified random sampling (StRS).

The equation describing stratified sampling is:

$$y_{ji} = y + sv_{ji} + e_{ji}$$

where \( i \) indexes each observation (within strata), 
\( j \) indexes each source of variation (strata), 
\( sv \) is the effect of the source variation, and 
\( y \) is the overall mean of observations.

If heterogeneity exists, stratifying will improve precision and reduce bias. StRS, therefore, typically results in a lower variance than SRS for a given fish population if the fish are not uniformly distributed over the sampling area. The variance of StRS is a weighted sum of the variances within each stratum.

With stratified sampling, the total population of \( A \) sampling units is divided into \( L \) subpopulations, each of which contains \( A_h \) sampling units. The total number of sampling units does not need to be equally distributed among the strata. In general, a random sample of size \( a \) is selected from the entire population of sampling units, of which \( a_h \) are allocated to each stratum using either equal, proportional, or Neymann (optimal) allocation.

For equal allocation:

$$a_1 = a_2 = ... = a_L .$$

For proportional allocation:

$$a_h = a \left( \frac{A_h}{A} \right).$$

For Neymann allocation, sample size in each stratum is determined by the amount of variance in each stratum. Strata with high variance are sampled more intensely than those with low variance to increase precision of estimates from strata with high variance.

The sample mean within each stratum can be found using:

$$\bar{y}_h = \frac{\sum_{i=1}^{a} y_{ih}}{a_h} .$$
An unbiased estimate of the population mean across all strata can be found using:

$$\bar{y}_{str} = \sum_{h=1}^{L} \frac{A_h}{A} \bar{y}_{h} = \sum_{h=1}^{L} W_h \bar{y}_h$$

where \( W_h = \frac{A_h}{A} \).

Notice in the above equation that the sample mean of each stratum is multiplied by the relative weight of that stratum. With stratified random sampling, simply using the arithmetic mean of the sample observations across all strata (as in SRS) will result in a biased estimate of the population mean if the fish are not uniformly distributed, unless stratified sampling occurs with proportional allocation.

For stratified random samples, the variance of each stratum is estimated using:

$$s_h^2 = \frac{1}{a_h - 1} \sum_{i=1}^{a_h} (y_{hi} - \bar{y}_h)^2$$

and the variance of the entire sample (across all strata) is estimated using:

$$s_{str}^2 = \frac{1}{A^2} \sum_{h=1}^{L} A_h (A_h - a_h) \frac{s_h^2}{a_h} = \sum_{h=1}^{L} W_h^2 \frac{s_h^2}{a_h} (1 - f_h)$$

where \( f_h = \frac{a_h}{A_h} \).

The standard error of the population can be estimated with the following equation:

$$SE(\bar{y}_{str}) = \sqrt{\sum_{h=1}^{L} W_h^2 \frac{s_h^2}{a_h} (1 - f_h)}.$$
Example 2: Using the data from Example 1, calculate the mean catch per tow assuming the tow areas were stratified by depth. Five tows were made consecutively in each of 5 strata (i.e. tows 1-5 come from stratum 1, tows 6-10 from stratum 2, etc.). Each stratum has 30 stations total. Calculate the mean and variance for each stratum and for all strata combined. Calculate the combined mean and variance and compare with those from Example 1.

<table>
<thead>
<tr>
<th>Stratum 1</th>
<th>Catch per tow</th>
<th>Stratum 2</th>
<th>Catch per tow</th>
<th>Stratum 3</th>
<th>Catch per tow</th>
<th>Stratum 4</th>
<th>Catch per tow</th>
<th>Stratum 5</th>
<th>Catch per tow</th>
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</thead>
<tbody>
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<td>Tow Number</td>
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<td>8 6 14 6 20 11</td>
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<td>10 13 15 35 25 3</td>
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</table>

Within stratum results

<table>
<thead>
<tr>
<th>Stratum</th>
<th>Avg</th>
<th>Var</th>
<th>Stddev</th>
</tr>
</thead>
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<td>Stratum 4</td>
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Across stratum results

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</table>

The mean of the stratified sample is the same as the unstratified sample (from Example 1) because there is proportional allocation of samples across the strata. The variance and standard deviation of the stratified sample are less than 2% and less than 15%, respectively, of the unstratified sample.

Systematic Sampling

Systematic sampling is another commonly used technique. To collect a systematic sample, it must first be possible to arrange the population in some sort of order (e.g., numbered 1 to A). The first observation is selected at random, and subsequently every kth unit throughout the population is selected. For example, to collect a sample from 450 fish, randomly select a number from 1 to 10 (k = 10 in this example). Suppose 7 was the number randomly selected. The sample would therefore be composed of the fish numbered 7, 17, 27,….447.

For any given sampling frame, there are k different samples that can potentially be taken by using each of the different starting values between 1 and k. In the example above, 10 independent samples could be selected using different starting values between 1 and k = 10. Using a starting value of 3 instead of 7 would produce a sample that includes units 3, 13, 23,….443. Each of these 10 samples would have a sample size of $a = \frac{A}{k}$. 

IX - 6
Unfortunately, $\frac{A}{k}$ is not always evenly divisible, leading to different sample sizes for the different samples. Table 1 illustrates this point for a population of $A = 40$ and $k = 6$.

Table 1. Possible systematic samples and sample size for population of $A = 40$ and $k = 6$.

<table>
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<th>Sample 1</th>
<th>Sample 2</th>
<th>Sample 3</th>
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</table>

$a = 7$ $a = 7$ $a = 7$ $a = 7$ $a = 6$ $a = 6$

The effect of the difference in sample size is usually small, even for small $a$’s, and can most times be ignored for $a$’s larger than 50.

Systematic sampling has several advantages over SRS. Collecting a systematic sample is easier than collecting a random sample because there is only one randomly selected unit. Systematic sampling also ensures the collection of samples is distributed throughout the population and the precision of a systematic sample is often superior to SRS. Two major disadvantages exist under this scheme: (1) there is no reliable formula for estimating standard error of the mean, and (2) if a trend exists in the units, and the value of $k$ is equal to the period of the trend (or a multiple of it), the chance of a biased result is greatly increased. Systematic sampling should therefore be used when it is known that there is no trend inherent in the data, or the trend is known and its periodicity does not correspond with $k$.

The mean of a systematic sample is calculated using the same formula as the mean of a simple random sample, i.e.,

$$\bar{y} = \frac{1}{a} \sum_{i=1}^{a} y_i.$$

Similarly, the variance of a systematic sample is calculated in the same manner as that of a simple random sample, if only one sample is taken:

$$s^2 = \frac{\sum_{i=1}^{a} (y_i - \bar{y})^2}{(a - 1)}.$$
When more than one systematic sample is taken from a single population of sampling units, the unbiased estimate of the population variance is calculated using:

$$\hat{V\bar{A}R}(y_{sys}) = \frac{A-1}{A} s^2 - \frac{k(a-1)}{a} s^2_{way}$$

where $s^2_{way} = \frac{1}{k(a-1)} \sum_{i=1}^{k} \sum_{j=1}^{a} (y_{ij} - \bar{y}_i)^2$ is the variance among units that lie within the same systematic sample (similar to the “within” sums of squares in and ANOVA). In this equation, $j$ designates sampling units within a sample and $i$ designates the individual samples. Taking more than one systematic sample from the same sampling frame ensures homogeneity of the samples within the systematic design. If the means of the individual samples are equal, then homogeneity exists.

**Example 3:** Catch data (number of bushels) from a portion of an experimental scallop fishing trip are shown below. What would be the mean catch per tow if every fifth tow were sampled, starting with the second tow? Estimate the variance.

<table>
<thead>
<tr>
<th>Tow Number</th>
<th>Catch</th>
<th>Tow Number</th>
<th>Catch</th>
<th>Tow Number</th>
<th>Catch</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>9.5</td>
<td>21</td>
<td>12.5</td>
<td>41</td>
<td>15</td>
</tr>
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<td>2</td>
<td>12.75</td>
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<td>1</td>
<td>42</td>
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</tr>
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<td>3</td>
<td>5.25</td>
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<td>8</td>
<td>43</td>
<td>13.5</td>
</tr>
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<td>44</td>
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<tr>
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</tr>
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<td>21.5</td>
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<td>12</td>
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<td>18</td>
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<td>49</td>
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</tr>
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<td>5.5</td>
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<td>10.25</td>
</tr>
<tr>
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<td>16.5</td>
<td>31</td>
<td>15</td>
<td>51</td>
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</tr>
<tr>
<td>12</td>
<td>12.75</td>
<td>32</td>
<td>14.5</td>
<td>52</td>
<td>14.5</td>
</tr>
<tr>
<td>13</td>
<td>15.5</td>
<td>33</td>
<td>15.5</td>
<td>53</td>
<td>7.5</td>
</tr>
<tr>
<td>14</td>
<td>14</td>
<td>34</td>
<td>15.25</td>
<td>54</td>
<td>18.5</td>
</tr>
<tr>
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<td>15.5</td>
<td>35</td>
<td>16.5</td>
<td>55</td>
<td>14.5</td>
</tr>
<tr>
<td>16</td>
<td>12.75</td>
<td>36</td>
<td>14</td>
<td>56</td>
<td>18.75</td>
</tr>
<tr>
<td>17</td>
<td>12</td>
<td>37</td>
<td>13.75</td>
<td>57</td>
<td>17.5</td>
</tr>
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<td>18</td>
<td>20.75</td>
<td>38</td>
<td>19.75</td>
<td>58</td>
<td>5</td>
</tr>
<tr>
<td>19</td>
<td>14</td>
<td>39</td>
<td>15.75</td>
<td>59</td>
<td>15.5</td>
</tr>
<tr>
<td>20</td>
<td>13.5</td>
<td>40</td>
<td>13.75</td>
<td>60</td>
<td>12.5</td>
</tr>
</tbody>
</table>

$\bar{y} = 13.33$ bushels

$s^2 = 19.96$
Multistage sampling

Before sampling begins, it is necessary to define the sampling units and develop a comprehensive list of all sampling units. However, it is often difficult to define what your sampling unit is. Once the sampling unit is defined, a complete sampling frame may not be readily available (such as a list of all possible beach access sites for recreational fishing), or the available frame may be inadequate (using a telephone directory to sample households would not include unlisted numbers or households without phones). Multistage sampling is a convenient alternative sampling method that addresses these problems. It is similar to stratified random sampling, except that the clusters (levels) of sampling are externally homogeneous and internally heterogeneous.

To conduct multistage sampling, the population is divided into primary sampling units (PSU’s) that are readily definable and meet the criteria of a sampling unit. This makes it possible to list all PSU’s as a sampling frame rather than trying to list all members of the population in question. Within the PSU’s, secondary sampling units (SSU’s) are defined. If necessary, it is possible to define third (TSU’s) and higher levels of sampling. A sample is chosen by sampling each of the levels in turn. For example, a random sample of the PSU’s are chosen. Within each of the PSU’s that are chosen, collect a random sample of SSU’s. From each of the sampled SSU’s, a sample of TSU’s is collected, and so on.

Suppose you wanted to sample croaker biological characteristics from the commercial pound net fishery in the Chesapeake Bay. As mentioned before, individual croaker cannot be sampled adequately from the Bay population. You can, however, set up a multistage sampling protocol that will allow you to sample the croaker population. First, define a PSU, such as one day’s catch by one commercial pound net fisherman. The PSU can then be divided into SSU’s such as one box of fish from a given PSU, and TSU’s such as individual fish from the SSU’s. You can obtain a random sample of vessels, from each sampled vessel, collect a random sample of boxes, and from each sampled box, collect a random sample of fish. Length, weight, and sex information could then be obtained from the sampled croaker. You could also randomly sample one otolith (left or right) from each fish as quaternary sampling units.

Multistage sampling can be used when a sampling frame is not readily available for the units you wish to sample. It can also be used for convenience as it is typically cheaper than other types of sampling. However, the sample variance obtained through multistage sampling is no better than, and often larger than the variance obtained from simple random sampling, resulting in large confidence intervals for your estimates. Also, the lower sample size and consequent fewer degrees of freedom make it harder to detect differences in your tests. Equations for finding sample means and variances at each level of sampling can be found in Thompson (1992).

Resampling Methods

Many traditional parametric statistics techniques require that data conform to a normal distribution in order to derive estimates of variance using mathematical formulae. In the past few decades, however, new statistical methods have been developed which do not have these requirements. These methods require instead greatly increased sample size and therefore rely on
the increased computational power of computers. Resampling methods are computer-based methods for obtaining multiple independent data sets from the original empirical data set (e.g., field collected data). Resampling assumes that without complete population information, the information in a random sample of the population is the best indicator of the population, and that taking multiple samples from the original sample is an adequate substitute for taking multiple samples of the population. Resampling allows us to make multiple estimates of a parameter of interest, and therefore estimate the variance of that parameter which is not always possible using traditional analytical techniques.

**Bootstrap**

One resampling method used frequently in fisheries research is the bootstrap. The bootstrap procedure has three steps:

1. Observations from the original sample are pooled and resampled with replacement to obtain a bootstrap data set with the same number of observations. This is repeated a large number of times to develop a series of bootstrap samples.
2. The parameter of interest is calculated for each replicate sample.
3. The mean and variance for the parameter of interest is estimated using the distribution of replicate parameter estimates.

The bootstrap procedure can also be used for linear regression data. Regression is conducted on the original data set and the residuals computed. Bootstrap data sets are developed when the residuals are sampled randomly with replacement and added to the original observations. For each replicate, regression parameters are estimated, producing a distribution of each parameter from which the mean and variance can be estimated.

As the number of replicate samples increases, the frequency distribution of parameter estimates will stabilize. There is no minimum or maximum number of replicates that are required, but Krebs (1989) recommends 200 replicates as a starting point.

Confidence limits for bootstrap estimates can be calculated in two ways. The first is the standard analytical method, using the standard error calculated from the replicate samples. The second method, proposed by Efron (1982) and called the percentile method, simply truncates the frequency distribution from the bootstrap samples on both tails. For example, the 95% confidence interval is found by truncating the frequency distribution between the 2.5% and 97.5% values. This method requires fewer calculations, but can result in biased confidence limits.

Bootstrap samples are inherently biased. For a given population with mean $\mu$, a sample of this population will provide an estimate of the mean $\bar{x}$, the mean of a bootstrap $\bar{x}_B$ is not an estimate of $\mu$, but rather an estimate of $\bar{x}$. The bias of the original sample mean is calculated as:

$$\text{Bias}(\bar{x}_B) = \bar{x} - \mu$$
and the bias of the bootstrap mean is estimated as:

\[
\text{Bias}(\bar{x}_B) = \bar{x}_B - \bar{x}_s.
\]

A bias-adjusted bootstrap mean can be calculated using the equation:

\[
\text{Bias-adjusted bootstrap mean} = 2\bar{x}_s - \bar{x}_B.
\]

There is controversy as to whether the bias-corrected mean is more appropriate than the original estimate. With a large bias (e.g., greater than 10%), it is best to provide both estimates and clarify that the parameter estimates are more uncertain than the confidence bounds indicate.

**Example 4**: The following table contains catch-at-age data for striped bass (*Morone saxatilis*) between Maine and North Carolina. Use catch curve analysis to estimate total mortality \(Z\). Using the bootstrap procedure, develop a mean and confidence limit for \(Z\).

<table>
<thead>
<tr>
<th>Age</th>
<th>Number</th>
<th>ln(N)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.5</td>
<td>-0.69</td>
</tr>
<tr>
<td>2</td>
<td>98</td>
<td>4.58</td>
</tr>
<tr>
<td>3</td>
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<td>551</td>
<td>6.31</td>
</tr>
<tr>
<td>6</td>
<td>476</td>
<td>6.17</td>
</tr>
<tr>
<td>7</td>
<td>456</td>
<td>6.12</td>
</tr>
<tr>
<td>8</td>
<td>216</td>
<td>5.38</td>
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<tr>
<td>9</td>
<td>143</td>
<td>4.96</td>
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<td>71</td>
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<td>2.56</td>
</tr>
<tr>
<td>14</td>
<td>4.6</td>
<td>1.53</td>
</tr>
<tr>
<td>15+</td>
<td>2.6</td>
<td>0.96</td>
</tr>
</tbody>
</table>

The slope of the plot of ln(N) against age for the fully recruited age classes gives an estimate of \(Z\). For the given data, \(Z\) is estimated at 0.51. The frequency distribution of \(Z\) from 200 bootstrap samples is shown in the figure below. The average value of \(Z\), estimated from the bootstrap replicates, is \(Z = 0.05092\), and the variance is estimated to be \(s^2 = 0.00165\).
Another resampling method often used in fisheries is the jack knife. The jack knife method is based on resamples of the empirical data set with one observation removed. The first observation is removed and the parameters of interest are estimated. The first observation is replaced and the second observation removed, and the parameters are estimated again. This procedure is repeated for all observations, resulting in a set of jack knife data sets equal to the original number of observations in the empirical data set.

**Fishery Dependent and Independent Sampling Methods**

Fishery dependent sampling can be conducted by trained data collection agents from the shore, at the dock, or on the fishing vessel. Fishery dependent data can also be reported by the angler or fisherman who caught the fish, using a variety of methods, such as logbooks, catch cards, or phone interviews. Fishery independent sampling is conducted in the field, using a variety of methods and gears. For both fishery dependent and independent sampling, several things should be taken into consideration when choosing the sampling strategy. These include factors such as the resource being sampled, the type of data to be collected, the type of fishery, and the amount of labor and cost involved. A list of useful references for developing sampling strategies for both fishery dependent and independent surveys are listed at the end of this chapter.

**Recreational Fisheries**

Any person who has access to some sort of fishing gear can be a recreational fisherman, and fishing can occur from just about anywhere there is access to the water. Because of the large number of possible participants and access points, sampling frames for recreational fisheries are generally very difficult to develop. A sampling frame based on a list of licensed anglers is only
Fishery dependent sampling of recreational fisheries can be done through a variety of methods, depending on the data to be collected. Biological information about individual fish should be collected directly by a trained observer. This is also a good method to sample catch and effort, but can be very expensive if there is a large sampling frame.

A less expensive, but less reliable method for collecting catch and effort data is through telephone surveys. A major disadvantage of these methods is that there are several biases associated with self-reported data, such as prestige bias and non-reporting bias. Other disadvantages include potential misidentification of species and recall bias (being able to remember specifics of individual trips). Telephone survey sampling frames are also often under-represented.

A third method to collect catch and effort data is through logbooks and catch cards. This is the least expensive method, but can also be the least reliable. These methods require individual anglers to record their catch for a trip and submit the reporting form to the collection agency. Logbooks and catch cards have many of the same biases as telephone surveys, including prestige and non-reporting bias, as well as misidentification of species. Often, different data is collected using different sampling methods. For example, the recreational module of the Atlantic Coastal Cooperative Statistics Program (ACCSP) and the Marine Recreational Fisheries Statistics Survey (MRFSS) conducted by the National Marine Fisheries Service both implement access point interviews to obtain recreational catch information, and use random digit dialing of households to obtain recreational effort.

Commercial Fisheries

Commercial fisheries sampling frames typically consist of all vessels or fishermen participating in a fishery, or all dealers that buy, sell, or trade fish. A sampling frame might also consist of all ports where commercially caught fish are offloaded. These sampling frames are often developed using lists of registered vessels or dealers. Unfortunately, these lists are not always complete. For example, not all fisheries require vessels to be registered, or a vessel may be licensed in another area (e.g. another state) but fishing locally. A list of ports with commercial docks would not include the small scale fisherman who fishes from his private craft, offloads coolers at a public marina, and personally drives them to a known dealer. Using a list of dealers may not capture the harvest sold directly from the vessel to passers-by at the dock. Developing a complete sampling frame may require extensive effort, such as speaking with fishermen, dealers, and dock owners, and first hand observation of which vessels offload catch and where.
The sampling strategy chosen will depend on the size of the sampling frame, the characteristics of the units within the frame, the resources available to sample, and the type of data being collected. A small sampling frame may allow data to be collected from all sampling units, \textit{i.e.}, a census. A sampling frame of vessels may be stratified by vessel size (\textit{e.g.} length, tonnage, horsepower), gear used, area fished or a combination of these or other factors. Collection of specific information on the catch (\textit{i.e.}, other than just total catch or total effort) may require multistage sampling.

Fishery dependent sampling of a commercial fishery can be conducted either at the dock, on the fishing vessel, or using fisherman reporting methods such as logbooks and call-in systems. Sampling at the dock tends to be less time intensive, less costly, and less intrusive for the fishermen, but does not allow for data collection of discarded fish. Sampling typically occurs when the catch is being offloaded. If the catch is unsorted, a simple random sample of the catch is usually sufficient. For example, random brailles of fish from the fish hold, or random boxes or tubs of fish from the deck can be collected for sampling. It is a good idea to sample from all parts of the offload (beginning, middle, end) to account for any hidden or unexpected biases. If the catch has been sorted by species or size before offload, a stratified random (\textit{e.g.}, 2 boxes of small, medium, and large fish) or systematic (\textit{e.g.}, every third box) sampling approach could be used.

Sea sampling can be used to collect specific area, catch, and effort data, including information on discarded species. This method of sampling is very costly and labor intensive. Sampling on individual vessels usually occurs on unsorted catch and should be conducted on random tows, unless there is some knowledge of appropriate stratification. Determining which vessels to sample aboard can be done in a purely random fashion, or through stratified random sampling. Stratifications are often set up by vessel size (\textit{e.g.}, hold capacity, length, or horsepower), fishing gear used, area fished, or target species.

Logbooks can be used to collect commercial data from a large number of participants for very low cost relative to other sampling methods. The data collected is typically restricted to catch and effort information. Call-in systems report the same data, but on a much more timely basis. The potential for bias or misreporting is greater with fisherman reported data.

\textbf{Resource Surveys}

Fisheries resource surveys attempt to measure some aspect of a fish stock, such as population abundance or biomass. The fish within that stock, however, are not valid sampling units. Sampling frames are therefore usually developed by dividing the resource area into sampling units. One of the most common methods to develop a sampling frame for ocean surveys is to divide the survey area into grids of certain size, where each grid area represents a single sampling unit (\textit{e.g.}, trawl tow, long line set). For example, the New York State Peconic Bay small mesh trawl survey divides Peconic Bay into grids of 1 minute longitude by 1 minute latitude. Riverine surveys could be delineated by river mile. Sampling units can also be stratified by, for example, depth, substrate, or salinity.

Once the sampling frame is developed, sampling can begin using whichever sampling method is most appropriate. A sampling method commonly used during fisheries independent sampling is
fixed station sampling, where a set of stations are sampled each time sampling is conducted. Whereas random sampling is used to get an overall picture of the resource in a broad area at that time, fixed station sampling is used to monitor changes at specific locations over time. Sampling the same sites at the same time each year for abundance provides an index of abundance for those sites. It is then possible to track abundance over time at those sites and evaluate whether abundance is increasing, decreasing, or remaining stable.

Sampling methods for fisheries independent surveys depend on the question being asked, the resources available to conduct the sampling, how often sampling will be conducted, the gear used, the area to be sampled, and the species in question. Some commonly used gears for fisheries independent sampling include many of the commercial and recreational fishing gears (e.g. trawls, gill nets, hook and line), beach seines, hydro-acoustics, and chemicals.

**Effort Standardization**

The two variables that fishery scientists want to get a handle on are fishing mortality ($F$) and population size ($N$). Neither of these is easily measured directly. However, estimates of fishing effort ($f$) and catch per unit effort (CPUE or $U$), which are much easier to measure, can provide an index of $F$ and $N$, respectively.

The change in catch rate of a fishery over time is related to the fishing mortality rate and the abundance, or:

$$\frac{dC}{dt} = FN$$

where $\frac{dC}{dt}$ is the change in catch over time

$F$ is fishing mortality rate, and

$N$ is the abundance.

Measured over time, this can be rewritten as

$$C = F\bar{N}$$

Where $C$ is the catch and

$\bar{N}$ is the average abundance over the time period.

Values of $F$ and $\bar{N}$ are rarely known, but estimates of other parameters can be used as indicators of these values. Incorporating a conversion factor, fishing effort $f$ is related to fishing mortality $F$, by the equation:

$$F = qf$$
and CPUE can be used as an indicator of abundance $N$ using the equation:

$$\bar{N} = \frac{C}{qf} \quad \text{or} \quad \bar{N} = \frac{1}{q} \bar{U}$$

where $q$ is the catchability coefficient.

Because $f$ and $U$ provide only an index of $F$ and $N$, there is no absolute correct unit of measure for these parameters. Any unit that gives a meaningful relationship is sufficient. The choice of unit often depends on how the fishery operates. For example, measuring the amount of time a gear is in the water may be an appropriate unit of effort for a trawl, gill net, or long line, but not necessarily for a purse seine where much of the effort is spent in searching for adequate schools of fish.

When comparing data from different surveys, different fisheries, or even different sectors of the same fishery, it is necessary to standardize the data to a common unit of effort. Often, it is even necessary to standardize effort for a single vessel over time since changes in technology, vessel characteristics, and crew can result in changes in fishing power.

Fishing mortality generated by each use of a certain gear is a function of three things:

1. The size of the area influenced by the gear in a single unit of effort,
2. The proportion of fish in that area that are retained by the gear, and
3. The ratio of the fish density in the area relative to the average density in the whole area inhabited by the stock (Gulland 1983).

Effort could therefore be standardized based on any of these three factors. In practice, the fishing effort data most commonly collected is the product of 1 and 2 above. This can be further broken down into the amount of time (or number of times) the gear is active and fishing power, which is the product of the area affected by the gear and the efficiency of the gear.

Standardizing effort therefore requires information on fishing power of individual units, measures of fishing time or number of operations, and the geographical distribution of fishing relative to fish.

If you are interested in comparing the relative effectiveness of two gears, then it is necessary to deploy the gear on the same densities of fish. If, however, you are looking at the effect of the gear on the stock, then it necessary to deploy the gear on the same stock, area, or other subdivision of the stock in question.

The simplest case in which to standardize effort is using two similar gears, of which one is considered the standard gear. Fishing power can be measured quantitatively for a given gear by dividing the catch per unit effort of that gear by the CPUE of the standard gear. In other words,
\[ P_i = \frac{C_i}{f_i} \frac{f_s}{C_s} = \frac{U_i}{U_s} \]

where \( i \) and \( s \) represent the \( i \)th and standard gears,
\( P \) is fishing power,
\( C \) is catch,
\( f \) is fishing effort, and
\( U \) is catch per unit effort.

Since power of the standard gear is assumed to be 1.0, this ratio of CPUEs provides the conversion factor used to standardize effort of the non-standard gear to the effort of the standard gear.

When using data from more than one comparison of the standard and non-standard gears, Gulland (1983) suggests using a log transformation of the data since catches often have a log-normal distribution. Average power is therefore estimated as:

\[ \log \bar{P}_i = \frac{1}{n} \sum_{j=1}^{n} \log P_{ij} = \frac{1}{n} \sum_{j=1}^{n} \log \left( \frac{U_{ij}}{U_{sj}} \right) \]

where \( U_{ij} \) and \( U_{sj} \) are the catches per unit effort of the \( i \)th and standard vessels on the \( j \)th of \( n \) comparisons.

Commonly, there are few direct comparisons between a given gear or vessel and the standard, and the correction factors for standardizing effort will therefore be highly variable. In order to reduce the variability, it is possible to designate more than one gear as standard if they are very similar, or use intermediate comparisons (first compare A with B then compare B with C as a means to compare gears A and C). Mathematically, this is expressed as:

\[ P_i = \frac{P_{i}}{P_a} \cdot \frac{P_a}{P_s} = \frac{U_{ij}}{U_{aj}} \cdot \frac{U_{ak}}{U_{sk}} \]

where gears \( i \) and \( a \) are compared at time \( j \), and gear \( a \) is compared to the standard gear \( s \) on another occasion, \( k \). This method of comparison is discussed by Robson (1966).
Exercises

1. The following table contains trawl survey catch per tow data. Calculate the mean catch per tow (in terms of number caught and weight caught) for the sampled area, assuming a simple random sample of tows was collected from a total of 500 possible stations. Calculate the variance, standard deviation, and standard error of the mean.

<table>
<thead>
<tr>
<th>Depth code</th>
<th>Number caught</th>
<th>Weight caught</th>
<th>Depth code</th>
<th>Number caught</th>
<th>Weight caught</th>
<th>Depth code</th>
<th>Number caught</th>
<th>Weight caught</th>
</tr>
</thead>
<tbody>
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<td>1</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
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<td>0</td>
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<td>0</td>
<td>0</td>
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<td>5</td>
<td>95</td>
<td>26.3</td>
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<td>43</td>
<td>8.4</td>
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</table>
2. Using the data from Example 1, calculate the mean catch per tow (for number caught and weight caught) assuming the tow areas were stratified by depth (depth code). Allocation of samples is shown in the table below. Calculate the mean and variance for each stratum and for all strata combined. Compare the combined mean and variance with those from Example 1.

<table>
<thead>
<tr>
<th>Depth code</th>
<th>Depth range</th>
<th>Number of possible tows in stratum</th>
<th>Number of tows made</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>≤ 30 feet</td>
<td>115</td>
<td>24</td>
</tr>
<tr>
<td>2</td>
<td>31-60 feet</td>
<td>145</td>
<td>29</td>
</tr>
<tr>
<td>3</td>
<td>61-90 feet</td>
<td>75</td>
<td>13</td>
</tr>
<tr>
<td>4</td>
<td>91-120 feet</td>
<td>75</td>
<td>11</td>
</tr>
<tr>
<td>5</td>
<td>121-180 feet</td>
<td>75</td>
<td>14</td>
</tr>
<tr>
<td>6</td>
<td>&gt; 180 feet</td>
<td>15</td>
<td>4</td>
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<tr>
<td>Total</td>
<td></td>
<td>500</td>
<td>95</td>
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</table>
Bibliography


Background

Sequential population analysis utilizes existing stock abundance data grouped by age or length and specified fishing mortality rates to project future catches and stock abundances. Similarly, historical catch at age or length data, when combined with an assumed natural mortality, is used to provide retrospective estimates of fishing mortality rates and absolute stock abundance.

Thompson and Bell (1934) used the growth and mortality equations to predict future yields from the Pacific halibut fishery. Later, Beverton and Holt (1957) developed an analytical solution to the yield per recruit model to predict the yield from a specific number of recruits given specified growth and mortality coefficients, and pattern of recruitment to the fishery.

Age-structured models including virtual population analysis and cohort analysis utilize catch or catch per unit effort at age data to reconstruct the population dynamics of exploited fish stocks, providing estimates of mortality rates and absolute population abundance. The age and length structured models provide a clear advantage over stock-production (Schaefer 1954) and dynamic pool (Beverton and Holt 1957) models in that these latter, more traditional models require data on effort, catchability or gear selectivity.

Baranov (1918) was the first fisheries scientist to propose the approach of applying data describing the age structure of the catch in order to calculate the contribution of each cohort in the stock to each year’s total catch. 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 and 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 age-structured model, and 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 at one-year intervals. 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. Catch at age data were analyzed one cohort at a time. Parameter values were estimated from 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- and year-specific coefficients.

Age-structured models have evolved considerably in the last several decades. Boot-strapping statistical methods have been added to provide estimates of uncertainty to the basic deterministic equation. The terms virtual population analysis (VPA) is used to describe the generic Fry and Doubleday models. Pope’s approximation is referred to as “cohort analysis.” All these models are part of the general class of models more appropriately referred to as sequential population analysis (SPA). Megrey (1989) provides a comprehensive review and comparison of all SPA type models from both theoretical and applied points of view.

Additional data from research vessel surveys are used to “tune” SPA models, by providing multiple inputs on age-specific indices of relative population abundance. The results of SPA models can be combined with recruitment indices to project future population abundance and potential catches for given level of fishing mortality.

**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).
The fish also grow rapidly ($K = 1.0$) to a maximum length of 40 cm, and reach 25 cm at age 1 (Figure 2).
Age-based projection models are based on the exponential decay model and the Baranov catch equation.

The exponential decay model is:

\[ N_t = N_0 e^{-(F_1 + M)t} = N_{t-1} e^{-Z_t} = N_{t-1} e^{-(F + M)} = N_{t-1} e^{-Z} \]

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:

\[ S = \frac{N_t}{N_{t-1}} = e^{-Z_t} = e^{-(F + M)} \]

The Baranov catch equation is:

\[ C_t = N_t \left( \frac{F_t}{Z_t} \right) (1 - e^{-Z_t}) \]

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 
\( (1 - e^{-Z}) \) is the mortality rate for the \( t \)th age.

Catch at age \( t \) is also estimated as:

\[ C_t = \left[ N_t - N_{t+1} \right] \frac{F_t}{Z_t} \]

**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 $N_t = N_0 e^{-(F+M)t}$, 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 $M = 0.7$.](image)

Table 1. Age-based projection of cohort abundance and catch.

<table>
<thead>
<tr>
<th>Year</th>
<th>Abundance $F = 0.0$</th>
<th>Abundance $F = 0.7$</th>
<th>Catch</th>
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<tbody>
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<td>500</td>
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</tr>
<tr>
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<td>188</td>
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<tr>
<td>3</td>
<td>123</td>
<td>30</td>
<td>46</td>
</tr>
<tr>
<td>4</td>
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<td>3</td>
</tr>
<tr>
<td>6</td>
<td>15</td>
<td>0.5</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Total Catch</td>
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<td>250</td>
</tr>
</tbody>
</table>

**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:

$$N_t = N_0 e^{-Z t} = N_0 e^{-(F_t + M_t) t}$$
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  $t$,
$L_\infty$ is the maximum length, and
$K$  is the growth coefficient.

This results in:

$$N_t = N_0 e^{-2\left[-\frac{1}{K} \ln\left(1 - \frac{L_t}{L_\infty}\right)\right]}$$

because the simplified von Bertalanffy equation can be rearranged and solved for $t$:

$$\frac{L_t}{L_\infty} = (1 - e^{-Kt})$$

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

$$-\ln\left(\frac{L_t}{L_\infty} - 1\right) = -Kt$$

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

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.

$$N_t = N_0 e^{-M\left(-\left(\frac{1}{K} \ln\left(1 - \frac{L_t}{L_\infty}\right)\right)\right)}$$

$$N_t = 1000 e^{-0.7\left(-\left(\frac{1}{L_{10}} \ln\left(1 - \frac{L_t}{L_\infty}\right)\right)\right)}$$

Where  $L_t$  is 0, 5, 10, 15, 20, 25, 30, 35, and 40 cm.
(B) Now consider the effect of adding an equal amount of fishing 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).
Table 2. Length-based projection of cohort abundance and catch.

<table>
<thead>
<tr>
<th>Length</th>
<th>Abundance $F = 0.0$</th>
<th>Abundance $F = 0.7$</th>
<th>Catch</th>
</tr>
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<td>Total Catch</td>
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</tr>
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**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:

$$N_t = \frac{C_t Z_t}{F_t \left(1 - e^{-Z_t}\right)}$$

$$N_t = \frac{C_t (F_t + M)}{F_t \left(1 - e^{-(F_t + M)}\right)} \ast.$$  

The fishing mortality rate for the $t$th age is estimated using the catch from the $t$th 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:

$$N_t = \frac{N_{t+1}}{e^{-Z_t}}$$

$$N_{t+1} \frac{1}{e^{-Z_t}} = \frac{C_t Z_t}{F_t \left(1 - e^{-Z_t}\right)}.$$
The equation is rearranged and expanded with unknown $F_t$s on one side of the equation for iterative solving:

$$\frac{N_{t+1}}{C_t} = \left[ (F_t + M) e^{-(F_t + M)} \right] / F_t \left( 1 - e^{-(F_t + M)} \right)$$

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:

$$N_t = \frac{C_t (F_t + M)}{F_t \left(1 - e^{-(F_t + M)}\right)} \cdot *$$

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:

$$N_t = \left[ (N_{t+1}) \left(e^{M/2}\right) + C_t \right] e^{M/2} \cdot *$$

The fishing mortality rate at the $t$th age is estimated by rearranging the exponential decay equation as follows:

$$N_{t+1} = N_t e^{-Z_t}$$

$$Z_t = \ln \left( \frac{N_{t+1}}{N_t} \right) = F_t + M$$

$$F_t = \ln \left( \frac{N_{t+1}}{N_t} \right) - M \cdot *$$

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 $x$th age during the $y$th year and of the $z$th year class or cohort.
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.

<table>
<thead>
<tr>
<th>Age</th>
<th>Catch</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
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</tr>
<tr>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>3</td>
<td>12</td>
</tr>
<tr>
<td>2</td>
<td>47</td>
</tr>
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<td>1</td>
<td>188</td>
</tr>
<tr>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

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.

\[
N_5 = \frac{C_5(Z_5)}{F_5\left(1 - e^{-Z_5}\right)} = \frac{C_5(F_5 + M)}{F_5\left(1 - e^{-(F_5 + M)}\right)}
\]

\[
N_5 = \frac{1(1.4)}{0.7(1 - e^{-1.4})}
\]

\[
N_5 = \frac{1.4}{0.7(1 - 0.25)} = \frac{1.4}{0.5} = 3
\]
Step (2) The fishing mortality rate at age 4 fish is estimated by iteratively solving the combined exponential decay and catch equation.

\[ \frac{N_4}{C_4} = \frac{3}{3} = \frac{(F_4 + M)e^{-(F_4+M)}}{F_4(1 - e^{-(F_4+M)})} \]

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.

\[ N_4 = \frac{C_4Z_4}{F_4(1 - e^{-Z_4})} = \frac{C_4(F_4 + M)}{F_4(1 - e^{-(F_4+M)})} \]

\[ N_4 = \frac{3(0.56 + 0.7)}{0.56(1 - e^{-(0.56+0.7)})} \]

\[ N_4 = \frac{3(1.26)}{0.56(1 - 0.28)} = \frac{3.78}{0.40} = 9 \]

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:

<table>
<thead>
<tr>
<th>Age</th>
<th>Catch</th>
<th>Estimated N</th>
<th>Actual N</th>
<th>Estimated F</th>
<th>Actual F</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
<td>1049</td>
<td>1000</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>1</td>
<td>188</td>
<td>521</td>
<td>491</td>
<td>0.66</td>
<td>0.70</td>
</tr>
<tr>
<td>2</td>
<td>47</td>
<td>134</td>
<td>122</td>
<td>0.64</td>
<td>0.70</td>
</tr>
<tr>
<td>3</td>
<td>12</td>
<td>35</td>
<td>30</td>
<td>0.62</td>
<td>0.70</td>
</tr>
<tr>
<td>4</td>
<td>3</td>
<td>9</td>
<td>7</td>
<td>0.56</td>
<td>0.70</td>
</tr>
<tr>
<td>5</td>
<td>1</td>
<td>3</td>
<td>2</td>
<td>0.70</td>
<td>0.70</td>
</tr>
</tbody>
</table>

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.
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.

\[ N_5 = \frac{C_5}{F_5/(F_5 + M)} \left[ 1 - e^{-(F_5 + M)} \right] \]

\[ N_5 = \frac{1}{0.7 / (0.7 + 0.7)} \left[ 1 - e^{-(0.7 + 0.7)} \right] \]

\[ N_5 = \frac{1}{0.7 / 1.4} (1 - 0.25) \]

\[ N_5 = \frac{1}{0.5 \times 0.753} = \frac{1}{0.375} = 2.65 \]

\[ N_4 = \left[ \left( \frac{M}{e^{M/2}} \right) + C_4 \right] e^{M/2} \]

\[ N_4 = \left[ (2.65 \left( e^{0.7/2} \right) + 3 \right] e^{0.7/2} \]

\[ N_4 = (3.76 + 3) \times 0.42 = 9.60 \]

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:

<table>
<thead>
<tr>
<th>Age</th>
<th>Catch</th>
<th>Estimated N</th>
<th>Actual N</th>
<th>Estimated F</th>
<th>Actual F</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>1</td>
<td>3</td>
<td>2</td>
<td>0.70</td>
<td>0.70</td>
</tr>
<tr>
<td>4</td>
<td>3</td>
<td>10</td>
<td>8</td>
<td>0.59</td>
<td>0.70</td>
</tr>
<tr>
<td>3</td>
<td>12</td>
<td>36</td>
<td>31</td>
<td>0.63</td>
<td>0.70</td>
</tr>
<tr>
<td>2</td>
<td>47</td>
<td>140</td>
<td>125</td>
<td>0.65</td>
<td>0.70</td>
</tr>
<tr>
<td>1</td>
<td>188</td>
<td>549</td>
<td>500</td>
<td>0.67</td>
<td>0.70</td>
</tr>
<tr>
<td>0</td>
<td>0</td>
<td>1105</td>
<td>1000</td>
<td>0.00</td>
<td>0.00</td>
</tr>
</tbody>
</table>
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:

<table>
<thead>
<tr>
<th>Harvest Year</th>
<th>Catch at Age</th>
<th>Total Catch</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>1990</td>
<td>$C_{0,90,90}$</td>
<td>$C_{1,90,89}$</td>
</tr>
<tr>
<td>1991</td>
<td>$C_{0,91,91}$</td>
<td>$C_{1,91,90}$</td>
</tr>
<tr>
<td>1992</td>
<td>$C_{0,92,92}$</td>
<td>$C_{1,92,91}$</td>
</tr>
<tr>
<td>1993</td>
<td>$C_{0,93,93}$</td>
<td>$C_{1,93,92}$</td>
</tr>
<tr>
<td>1994</td>
<td>$C_{0,94,94}$</td>
<td>$C_{1,94,93}$</td>
</tr>
<tr>
<td>1995</td>
<td>$C_{0,95,95}$</td>
<td>$C_{1,95,94}$</td>
</tr>
<tr>
<td>1996</td>
<td>$C_{0,96,96}$</td>
<td>$C_{1,96,95}$</td>
</tr>
</tbody>
</table>

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:

<table>
<thead>
<tr>
<th>Harvest Year</th>
<th>Abundance at Age</th>
<th>Total Stock Abundance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>1990</td>
<td>$N_{0,90,90}$</td>
<td>$N_{1,90,89}$</td>
</tr>
<tr>
<td>1991</td>
<td>$N_{0,91,91}$</td>
<td>$N_{1,91,90}$</td>
</tr>
<tr>
<td>1992</td>
<td>$N_{0,92,92}$</td>
<td>$N_{1,92,91}$</td>
</tr>
<tr>
<td>1993</td>
<td>$N_{0,93,93}$</td>
<td>$N_{1,93,92}$</td>
</tr>
<tr>
<td>1994</td>
<td>$N_{0,94,94}$</td>
<td>$N_{1,94,93}$</td>
</tr>
<tr>
<td>1995</td>
<td>$N_{0,95,95}$</td>
<td>$N_{1,95,94}$</td>
</tr>
<tr>
<td>1996</td>
<td>$N_{0,96,96}$</td>
<td>$N_{1,96,95}$</td>
</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>Harvest Year</th>
<th>Fishing Mortality at Age</th>
<th>Total Fishing Mortality</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>1990</td>
<td>$F_{0,90,90}$</td>
<td>$F_{1,90,89}$</td>
</tr>
<tr>
<td>1991</td>
<td>$F_{0,91,90}$</td>
<td>$F_{1,91,90}$</td>
</tr>
<tr>
<td>1992</td>
<td>$F_{0,92,90}$</td>
<td>$F_{1,92,90}$</td>
</tr>
<tr>
<td>1993</td>
<td>$F_{0,93,92}$</td>
<td>$F_{1,93,91}$</td>
</tr>
<tr>
<td>1994</td>
<td>$F_{0,94,93}$</td>
<td>$F_{1,94,92}$</td>
</tr>
<tr>
<td>1995</td>
<td>$F_{0,95,94}$</td>
<td>$F_{1,95,93}$</td>
</tr>
<tr>
<td>1996</td>
<td>$F_{0,96,94}$</td>
<td>$F_{1,96,95}$</td>
</tr>
</tbody>
</table>

**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).

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:
\[ N_t = N_{t_0}e^{\Delta t} + C_tM^{N/2} \]

where \( \Delta t \) is the time required to grow from the beginning to the end of a length interval, and \( \Delta t \) is estimated from the rearranged von Bertalanffy growth equation.

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

Computationally, the length intervals are first specified over the full length range of the fish, then the \( \Delta t \) are estimated for each length range. At smaller lengths, the \( \Delta t \) are small, and at larger lengths, the \( \Delta t \) are large. Using the time interval (\( \Delta t \)) 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.

<table>
<thead>
<tr>
<th>Length</th>
<th>Catch</th>
</tr>
</thead>
<tbody>
<tr>
<td>40-44</td>
<td>53</td>
</tr>
<tr>
<td>35-39</td>
<td>88</td>
</tr>
<tr>
<td>30-34</td>
<td>110</td>
</tr>
<tr>
<td>25-29</td>
<td></td>
</tr>
<tr>
<td>20-24</td>
<td></td>
</tr>
<tr>
<td>15-19</td>
<td></td>
</tr>
<tr>
<td>10-14</td>
<td></td>
</tr>
<tr>
<td>5-9</td>
<td></td>
</tr>
<tr>
<td>0-4</td>
<td></td>
</tr>
</tbody>
</table>

Total catch: 251 fish over the size range of the cohort

The time interval (\( \Delta t \)) for each length class is estimated using the rearranged von Bertalanffy growth function for the limits of each length class.
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.

\[
N_{35} = \frac{C_{35-39}}{F/Z_{(35-39)}}
\]

\[
N_{35} = \frac{53}{0.5} = 106
\]

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.

\[
N_{30} = \left[ N_{35} \left( e^{\frac{M \cdot \Delta t}{2}} \right) + C_{(30-34)} \right] e^{\frac{M \cdot \Delta t}{2}}
\]

\[
N_{30} = \left[ 106(1.2732) + 88 \right] \cdot 2.732
\]

\[
N_{30} = (224) \cdot 2.732 = 624
\]

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.

\[
\left( \frac{F}{Z} \right)_{(30-34)} = \frac{C_{(30-34)}}{N_{30} - N_{35}}
\]

\[
\left( \frac{F}{Z} \right)_{(30-34)} = \frac{88}{(284 - 106)} = \frac{88}{178} = 0.49
\]
Step (4)  
Fishing mortality for the second largest length class is estimated from the exploitation ratio and the assumed natural mortality.

\[
F_{(30-34)}^{(30-34)} = M \left[ \frac{F}{Z} \left(1 - \frac{F}{Z}\right) \right]^{(30-34)}
\]

\[
F_{(30-34)} = 0.7 \left[ 0.49 \left(1 - 0.49\right) \right] = 0.69
\]

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:

<table>
<thead>
<tr>
<th>Length</th>
<th>Catch</th>
<th>Estimated N</th>
<th>Actual N</th>
<th>Estimated F</th>
<th>Actual F</th>
</tr>
</thead>
<tbody>
<tr>
<td>35-39</td>
<td>53</td>
<td>106</td>
<td>108</td>
<td>0.70</td>
<td>0.70</td>
</tr>
<tr>
<td>30-34</td>
<td>88</td>
<td>284</td>
<td>284</td>
<td>0.68</td>
<td>0.70</td>
</tr>
<tr>
<td>25-29</td>
<td>110</td>
<td>504</td>
<td>506</td>
<td>0.70</td>
<td>0.70</td>
</tr>
<tr>
<td>20-24</td>
<td>617</td>
<td>613</td>
<td>613</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>15-19</td>
<td>721</td>
<td>720</td>
<td>720</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>10-14</td>
<td>819</td>
<td>816</td>
<td>816</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>5-9</td>
<td>913</td>
<td>913</td>
<td>913</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>0-4</td>
<td>1002</td>
<td>1000</td>
<td>1000</td>
<td>0.00</td>
<td>0.00</td>
</tr>
</tbody>
</table>

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:

<table>
<thead>
<tr>
<th>Harvest Year</th>
<th>Catch at Length</th>
<th>Total Catch</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>25-29</td>
<td>30-34</td>
</tr>
<tr>
<td>1990</td>
<td>(C_{25-29,90})</td>
<td>(C_{30-34,90})</td>
</tr>
<tr>
<td>1991</td>
<td>(C_{25-29,91})</td>
<td>(C_{30-34,91})</td>
</tr>
<tr>
<td>1992</td>
<td>(C_{25-29,92})</td>
<td>(C_{30-34,92})</td>
</tr>
<tr>
<td>1993</td>
<td>(C_{25-29,93})</td>
<td>(C_{30-34,93})</td>
</tr>
<tr>
<td>1994</td>
<td>(C_{25-29,94})</td>
<td>(C_{30-34,94})</td>
</tr>
<tr>
<td>1995</td>
<td>(C_{25-29,95})</td>
<td>(C_{30-34,95})</td>
</tr>
<tr>
<td>1996</td>
<td>(C_{25-29,96})</td>
<td>(C_{30-34,96})</td>
</tr>
</tbody>
</table>

where \(C_{x,y}\) is the catch during the \(y\)th year of the \(x\)th 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:

<table>
<thead>
<tr>
<th>Harvest Year</th>
<th>Abundance at Length</th>
<th>Total Stock Abundance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0-4</td>
<td>5-9</td>
</tr>
<tr>
<td>1990</td>
<td>(N_{0-4,90})</td>
<td>(N_{5-9,90})</td>
</tr>
<tr>
<td>1991</td>
<td>(N_{0-4,91})</td>
<td>(N_{5-9,91})</td>
</tr>
<tr>
<td>1992</td>
<td>(N_{0-4,92})</td>
<td>(N_{5-9,92})</td>
</tr>
<tr>
<td>1993</td>
<td>(N_{0-4,93})</td>
<td>(N_{5-9,93})</td>
</tr>
<tr>
<td>1994</td>
<td>(N_{0-4,94})</td>
<td>(N_{5-9,94})</td>
</tr>
<tr>
<td>1995</td>
<td>(N_{0-4,95})</td>
<td>(N_{5-9,95})</td>
</tr>
<tr>
<td>1996</td>
<td>(N_{0-4,96})</td>
<td>(N_{5-9,96})</td>
</tr>
</tbody>
</table>

where \(N_{x,y}\) is the estimated abundance during the \(y\)th year of the \(x\)th length interval.

A matrix of fishing mortality rates \(F_{x,y}\) also results from the sequential population analysis.
<table>
<thead>
<tr>
<th>Harvest Year</th>
<th>Fishing Mortality at Length</th>
<th>Average Fishing Mortality</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>25-29</td>
<td>30-34</td>
</tr>
<tr>
<td>1990</td>
<td>$F_{25-29,90}$</td>
<td>$F_{30-34,90}$</td>
</tr>
<tr>
<td>1991</td>
<td>$F_{25-29,91}$</td>
<td>$F_{30-34,91}$</td>
</tr>
<tr>
<td>1992</td>
<td>$F_{25-29,92}$</td>
<td>$F_{30-34,92}$</td>
</tr>
<tr>
<td>1993</td>
<td>$F_{25-29,93}$</td>
<td>$F_{30-34,93}$</td>
</tr>
<tr>
<td>1994</td>
<td>$F_{25-29,94}$</td>
<td>$F_{30-34,94}$</td>
</tr>
<tr>
<td>1995</td>
<td>$F_{25-29,95}$</td>
<td>$F_{30-34,95}$</td>
</tr>
<tr>
<td>1996</td>
<td>$F_{25-29,96}$</td>
<td>$F_{30-34,96}$</td>
</tr>
</tbody>
</table>
Exercises

1. The following catches were taken over the early portion of the lifespan of a cohort of fish in a pond.

<table>
<thead>
<tr>
<th>Age</th>
<th>Catch</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>100</td>
</tr>
<tr>
<td>2</td>
<td>500</td>
</tr>
<tr>
<td>3</td>
<td>300</td>
</tr>
<tr>
<td>4</td>
<td>200</td>
</tr>
</tbody>
</table>

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:

(a) Determine abundance-at-age and fishing mortality rate-at-age matrices for bluefish using cohort analysis due to its computational simplicity.

(b) 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.

(c) 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.
<table>
<thead>
<tr>
<th>Year</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
</tr>
</thead>
<tbody>
<tr>
<td>1982</td>
<td>7.001</td>
<td>12.493</td>
<td>4.633</td>
<td>2.504</td>
<td>2.297</td>
<td>2.418</td>
<td>1.368</td>
<td>1.050</td>
<td>0.538</td>
<td>0.281</td>
</tr>
<tr>
<td>1983</td>
<td>6.784</td>
<td>8.526</td>
<td>9.447</td>
<td>2.605</td>
<td>1.611</td>
<td>1.840</td>
<td>1.818</td>
<td>1.710</td>
<td>0.752</td>
<td>0.325</td>
</tr>
<tr>
<td>1984</td>
<td>8.719</td>
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<td>3.184</td>
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<tr>
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<td>1996</td>
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<td>2.528</td>
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<td>0.741</td>
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<td>0.447</td>
<td>0.231</td>
<td>0.042</td>
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</table>

\( M = 0.25 \)
Bibliography


Fry, F. E. 1957. Assessment and mortalities by the use of the virtual population. Proceedings of the ICNAF and FAO Meeting on Fishery Effort and the Effects of Fishery in Resources. 15 pp.


Background

Many fisheries stock assessment techniques require estimating the abundance of fish in the population. Ideally, population dynamics is concerned with how abundance changes over time and why. However, most marine fish are not observed directly, so we can never be sure how many fish there are. This is why many resource agencies devote major portions of their budgets to resource assessment, and minor portions to quantifying the ecological relationships among species.

Catch Survey Analysis

There are several types of relative abundance data that can be used to index trends in stock abundance:

- catch per unit effort;
- spawn deposition surveys;
- standardized trawl surveys;
- acoustic surveys, etc.

These all measure relative abundance and have an unknown calibration coefficient, or catchability. They can be calibrated to absolute abundance with a population model.

In 1980, the National Marine Fisheries Service (NMFS) had been conducting standardized trawl surveys for over 15 years but had not yet fully integrated the data into stock assessments, because of (1) high sampling variability of the survey, and (2) relative abundance needed to be converted to absolute abundance. The Catch Survey Analysis method of population estimation was developed to allow the incorporation of trawl survey data into stock assessments (Collie and Sissenwine 1983).

Catch Survey Analysis is derived from the classic depletion estimators of Leslie and DeLury. In the original DeLury model, catchability, $q$, is estimated from the decline in catch rate of a closed population (Figure 1). The DeLury method has since been modified to include recruitment and natural mortality, and has been adapted and used for several different species (Table 1). At the Woods Hole Laboratory, the Collie-Sissenwine method is referred to as the "Modified DeLury Method," or sometimes just the "DeLury method." Collie and Kruse (1998) introduced the term "Catch Survey Analysis" to distinguish this depletion method for open populations from the classic depletion estimators for closed populations of Leslie and DeLury.
Figure 1. Plot of catch per unit effort ($n_i/f_i$) versus the cumulative catch ($x_i$) for a lobster population: redrawn from DeLury (1947).

Table 1. Adaptations of the DeLury Method.

<table>
<thead>
<tr>
<th>Author</th>
<th>Year</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>DeLury</td>
<td>1947</td>
<td>Lobster</td>
</tr>
<tr>
<td>Allen</td>
<td>1966</td>
<td>Fin whale</td>
</tr>
<tr>
<td>Collie and Sissenwine</td>
<td>1983</td>
<td>Flounder, haddock</td>
</tr>
<tr>
<td>Kruse and Collie</td>
<td>1991</td>
<td>Red king crab</td>
</tr>
<tr>
<td>Conser</td>
<td>1991</td>
<td>Atlantic sea scallop</td>
</tr>
<tr>
<td>Conser and Idoine</td>
<td>1992</td>
<td>American lobster</td>
</tr>
</tbody>
</table>

Derivation of the Collie-Sissenwine method

Let $P_t$ be the numerical abundance of post-recruit fish at the start of survey year $t$. For convenience, have the survey coincide with the start of the year. $R_t$ is the number of new recruits at the start of year $t$. The catch in numbers, $C_t$, is assumed to occur part way through year $t$. $T_t$ is the proportion of the year between the survey and fishery. The population dynamics model can be written as:

$$P_{t+1} = (P_t + R_t)e^{-M_t} - C_t e^{-M_t(1-T_t)}.$$

According to the population dynamics model, post-recruits ($P$) in year $t+1$ are the sum of recruits ($R$) and post-recruits in year $t$ discounted by natural mortality ($M_t$), minus the commercial catch ($C_t$) also discounted for natural mortality between the time of the survey and the time of the commercial fishery ($T_t$). Note that annual estimates of $M_t$ and $T_t$ are used where known.
The survey measures relative abundance, not absolute abundance. The two are related with an observation model. Relative abundance is assumed proportional to absolute abundance with a survey catchability coefficient, \( q \). Phi, \( \phi \), denotes recruit catchability relative to post-recruits; \( \phi < 1 \) would indicate that recruits are less catchable than post-recruits. The observation model can be written as:

\[
p_r = q P_r \times \text{observation error}
\]

for relative abundance of post-recruits and

\[
r_t = q NR_t \times \text{observation error}
\]

for relative abundance of recruits (note that a full age structure is not required).

The original population model is rewritten in units of relative abundance. Substituting and multiplying by \( q \) (survey catchability coefficient)

\[
p_{(t+1)} = (p_t + r_t/\phi)e^{-M_t} - qC_t e^{-M_t(1-\tau_t)} + \varepsilon_t,
\]

where \( \varepsilon \) is a process error. This equation can be rearranged as a linear function of \( q \):

\[
(p_t + r_t/\phi)e^{-M_t} - p_{t+1} = qC_t e^{-M_t(1-\tau_t)} + \varepsilon_t
\]

which is of the form \( Y = bX + \varepsilon \). If all process error is assumed, linear regression with zero intercept can be used for an initial estimate of \( q \), but the measurement errors may be confounded in the \( Y \) term.

**Fitting the Collie-Sissenwine Method to Data**

If we assume an all observation-error model:

<table>
<thead>
<tr>
<th>Year</th>
<th>Obs.</th>
<th>Est.</th>
<th>Est.</th>
<th>Obs.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>( r_1 )</td>
<td>( \hat{r}_1 )</td>
<td>( \hat{p}_1 )</td>
<td>( p_1 )</td>
</tr>
<tr>
<td>2</td>
<td>( r_2 )</td>
<td>( \hat{r}_2 )</td>
<td>( \hat{p}_2 )</td>
<td>( p_2 )</td>
</tr>
<tr>
<td>3</td>
<td>( r_3 )</td>
<td>( \hat{r}_3 )</td>
<td>( \hat{p}_3 )</td>
<td>( p_3 )</td>
</tr>
<tr>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>-</td>
<td>-</td>
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</tr>
<tr>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>( n )</td>
<td>( r_{n-1} )</td>
<td>( \hat{r}_{n-1} )</td>
<td>( \hat{p}_{n-1} )</td>
<td>( p_{n-1} )</td>
</tr>
<tr>
<td>( n )</td>
<td>( r_n )</td>
<td></td>
<td>( \hat{p}_n )</td>
<td>( p_n )</td>
</tr>
</tbody>
</table>
Number of observations: \( n \)  
Number of parameters to estimate \( \{r_1, r_2, \ldots, r_{n-1}, p_1, q\} \): \(-(n + 1)\)  
Degrees of freedom: \( n - 2 \)

Observed relative abundance is equal to the true but unknown relative abundance times a measurement error. This can be written mathematically as:

\[
\tilde{p}_t = p_t e^{\eta_t} \quad \text{and} \quad \tilde{r}_t = r_t e^{\delta_t}
\]

where \( \tilde{p}_t \) and \( \tilde{r}_t \) are the observed number of post-recruits and recruits, respectively, and \( \eta \) and \( \delta \) are normally distributed measurement errors.

These residual errors are minimized by weighted non-linear least squares.

\[
MIN \left[ \sum_{t=1}^{n} \eta_t^2 + w \sum_{t=1}^{n-1} \delta_t^2 \right]
\]

where \( w \) is a weighting factor. This equation can be rewritten as:

\[
MIN \left[ \sum_{t=1}^{n} (\ln p_t - \ln \hat{p}_t)^2 + w \sum_{t=1}^{n-1} (\ln r_t - \ln \hat{r}_t)^2 \right]
\]

and can be minimized by nonlinear estimation. The original implementation of this method was the FORTRAN program DELPOP (Collie and Sissenwine 1983). An APL version was implemented by Conser (1991) and a Splus version also has been written. The minimization can be performed with a spreadsheet (e.g. EXCEL using Solver function) but without the diagnostics provided by the computer programs. The parameters \( M, T, \) and \( \phi \) are input, and \( q \) is estimated along with the sequence of relative abundance \( (r_t, p_t) \) that best matches the observed relative abundance.

The absolute abundances can then be reconstructed with

\[
\hat{R}_t = \frac{\hat{r}_t}{\hat{q} \phi} \quad \text{and} \quad \hat{P}_t = \frac{\hat{p}_t}{\hat{q}}.
\]

The harvest rate, \( h \), of the recruited population is,

\[
h_t = \frac{C_t}{(R_t + P_t)e^{-M_tT_t}}.
\]
In the original Collie-Sissenwine formulation, we fit a mixed-error model with both measurement errors and process errors. In recent studies (Collie and Kruse 1998) we have used an all measurement-error structure. There are two reasons for omitting process errors.

1. The mixed-error model required estimating more parameters, which may overparameterize the problem; we found problem data sets that would not converge.

2. In comparing the mixed-error and measurement-error structures for Kodiak red king crabs, we obtained virtually identical population estimates.

Applying the Collie-Sissenwine Method to King Crabs

The Alaskan king crab supported one of the most lucrative invertebrate fisheries, and despite declining stocks, continues to be a valuable fishery. Most red king crab fisheries in Alaska are managed with an exploitation-rate strategy, in which annual catches are prescribed by applying a harvest rate toward an estimate of exploitable male biomass.

King crab abundance has been estimated with annual stock assessment surveys. Since the 1970s the NMFS has assessed Bering Sea stocks with trawl surveys. Survey relative abundance is calibrated to absolute abundance with the area swept method. In the Gulf of Alaska, relative abundance indices were estimated from pot surveys conducted by the Alaska Department of Fish and Game (ADFG) during the 1970s and 1980s. For a few stocks, absolute abundances of legal males were calculated with mark-recapture studies. Since the mid 1980s, Gordon Kruse of the ADFG has been investigating and promoting the use of alternative methods of population assessment, particularly those incorporating a population model.

One such method is catch-survey analysis, which calibrates relative abundance to absolute abundance and smoothes variability in the relative abundance data. We applied this method to two king crab stocks: one residing in Bristol Bay in the eastern Bering Sea and one around Kodiak in the Gulf of Alaska. Although absolute abundance is estimated in the Bering Sea, the area-swept calibration is open to question. In the Gulf of Alaska, the survey catchability clearly needs to be estimated. Hereafter, we refer to the two stocks as Bristol Bay and Kodiak.

In the penultimate paragraph of the Collie and Sissenwine paper, we recommended that the reliability of the estimation procedure be tested on simulated data sets for which the true abundance is known. This study provided an opportunity to test the method with Monte Carlo simulations.

The standard length measurement for the red king crab, *Paralithodes camtschaticus*, is from the right eye to the posterior margin of the carapace. King crabs cannot be aged, but they can be classified into recruits and post-recruits based on their size and shell age. For Bristol Bay, a legal king crab is a male greater than 135 mm carapace length. King crabs have an annual molt cycle but males do not necessarily molt every year once they reach legal size. Crabs that molt have new shells; ones that do not molt have old shells. Recruits are new shell crabs between legal size and one mean growth increment larger than the legal size (Table 2). Post-recruits are all
remaining legal crabs. The use of shell age makes king crabs an ideal species for catch-survey analysis.

<table>
<thead>
<tr>
<th>Table 2. Dynamics of size and shell age for king crabs.</th>
</tr>
</thead>
<tbody>
<tr>
<td>new shell</td>
</tr>
<tr>
<td>Recruit</td>
</tr>
<tr>
<td>Post-recruit</td>
</tr>
<tr>
<td>+ 1 molt</td>
</tr>
<tr>
<td>Size (mm) →</td>
</tr>
<tr>
<td>old shell</td>
</tr>
<tr>
<td>legal size</td>
</tr>
<tr>
<td>Post-recruit</td>
</tr>
<tr>
<td>+ 1 molt</td>
</tr>
</tbody>
</table>

Although several transitions are possible between the four categories, a recruit must always become a post-recruit the next year.

**Bristol Bay**

The first application is for Bristol Bay red king crabs. Crabs are sampled during annual trawl surveys in mid-June. The crab fishery opens around the beginning of October. The timing of these events is shown in Figure 2.

Figure 3 shows the results of the catch-survey analysis for Bristol Bay. The points are the observed relative abundances; the lines are the values estimated with either constant natural mortality or a sequence of natural mortality rates estimated by Zheng et al. (1995) with a length-based model. Note that post-recruits are offset by one year from the recruits, as they should be.

With the constant $M$ fit, there is a pattern in the residuals. In early and later years the model over-predicts recruits and under-predicts post-recruits; in middle years the opposite is true. This pattern indicates that natural mortality was higher from 1982 to 1986. The variable $M$ fit accounts for this shift and fits the observed data much better in these middle years.

Notice that the model smoothes out year-to-year variability in the abundance estimates. This is important because a small increase or decrease can make the differences of the fishery being open or closed. Recruit abundance is not predicted in the final year because of the recursive
Figure 3. Abundances of Bristol Bay red king crabs measured with a trawl survey and estimated with catch-survey analysis. The constant natural mortality rate, $M$, was 0.36 and the variable $M$s are from Zheng et al. 1995. Adapted from Collie and Kruse (1998) with permission.
nature of the population equation. Of course the most recent year is the one of most interest to managers. To estimate legal abundance we must rely on observed recruits in the final year.

Figure 4 shows estimates of legal crab abundance superimposed on the survey data for comparison. Also shown is the commercial catch. The period from 1975 to 1980 was the king crab bonanza; the catch during these six years was worth $1 billion. The crash started in 1981; in 1983 the fishery was closed and continued at low levels until 1994 when only a small catch was taken around the Pribilof Islands. What caused the crash? A combination of high harvest rates and an apparent increase in natural mortality. With the variable natural mortality rate fit, harvest rates were still high leading up to the crash, but more of the deaths are attributed to natural causes. Recruits that were there one year disappeared by the next year. Natural mortality apparently increased to almost one. We have looked at several covariates (temperature and Pacific cod abundance) but neither of them has such a sharp pattern as the apparent $M$.

Next we tested how well the model performs with a known data set (Figure 5). We used the 20 years of data estimated for Bristol Bay as our test data set, fixing the survey catchability coefficient, $q$, at 1.0. First we tested how errors in the input parameters affect the estimation of the output parameters, especially $q$. We focus on $q$ because division of relative abundance by the wrong $q$ will result in biased absolute abundance estimates. In the top panel, we plot the estimate of $q$ relative to its known value of 1.0, with errors in the input parameters. The value of $q$ is insensitive to errors in specifying the timing of the commercial catch. Even though we specify an accurate annual value, the consequence of not doing so is minor. Likewise, discretizing a continuous catch would not be a problem. In this example, $T$ was constant at 0.25; increasing or decreasing the input $T$ did not affect the sum of squares because $e^{-T}$ is a constant multiplier of $q$.

The second panel of Figure 5 shows that estimates of $q$ are negatively correlated with $M$. “Poor-man’s confidence regions” were created by simply plotting the increase in sum of squares resulting from incorrect specification of $M$; the area of the polygon is proportional to the sum of squares. Values of $q$ are also negatively correlated with recruit catchability (bottom panel). In either case, we must substantially deviate from the known input value to appreciably change the sum of squares. The sum of squares of the fit to the actual data would be a much bigger circle than any of these shown. It is therefore unlikely that we can estimate $M$ or $\phi$ from real data sets in addition to $q$. These parameters are not structurally confounded, but their estimates will be strongly negatively correlated.
Figure 4. Legal male abundance, harvest rate, and natural mortality of Bristol Bay red king crabs. Adapted from Collie & Kruse (1998) with permission.
Figure 5. Sensitivity of the catch-survey analysis to errors in the input data. Each panel shows the deviation of the estimated catchability coefficient from its known value of 1 with errors in the input value of $T$ (true value = 0.25), $M$ (true value = 0.3), or $\phi$ (true value = 1). Larger circles indicate a poorer fit of the catch-survey analysis. Adapted from Collie & Kruse (1998) with permission.
Monte Carlo Simulations

The next step is to test how the magnitude and structure of the residual errors affects parameter estimation (Figure 6). The Monte Carlo simulations start with the same known data set with no error. The known data are modified with lognormally distributed random errors. We tested three types of error structure.

1. Measurement errors as assumed in fitting the model,
2. Correlated measurement errors as might occur because the observed \( r \) and \( p \) each year come from the same survey, and
3. Process errors, or errors in the population dynamics equation.

Regardless of the structure of the input error, we still fit the same measurement-error model. The results are stored and the randomization process repeated 200 times. Finally we summarize the bias and dispersion of the parameter estimates.

The box plots (Figure 7) summarize the distributions of the \( q \) estimates relative to the true value of 1.0. Shown are the medians, the quartiles, 1.5 times the interquartile distance, and outliers. The digits beneath each box indicate the type and magnitude of the error:

left: measurement-error standard deviation  
center: measurement-error correlation  
right: process-error standard deviation.

The distribution of estimated \( q \)’s is lognormal. Increasing the measurement-error standard deviation causes the distribution to be skewed downwards and to have greater dispersion.

Figure 8 illustrates the difference between measurement and process errors. In both panels the dots indicate the known post-recruit abundance with no error; in both cases the error standard deviation was 0.5. With measurement errors the distribution of post-recruit abundance fluctuates around the true values. With process errors, abundance goes off on excursions and is only tied to the true values because the correct recruitment is input each year. So we might expect the program to have more trouble reconstructing the true abundance, especially with an all measurement-error assumption.
Monte Carlo Simulations

Known Relative Abundance Data

Modify with Random Variability

Repeat 200 times

DELPOP Estimation

Summarize Bias and Dispersion of Estimates

Figure 6. Flow chart of the sequence of steps in the Monte Carlo simulation process.
Figure 7. Distributions of $q$ relative to true value of 1.0 in Monte Carlo simulations with different magnitudes of measurement error. Each box plot summarizes the distribution of 200 $q$ values. The white bar is the median and the box contains the second and third quartiles. The dotted line extends 1.5 times the interquartile distance and the horizontal lines are outliers. The three numbers under each box indicate the standard deviation of measurement errors, the correlation of measurement errors, and process error standard deviation (from left to right). Adapted from Collie & Kruse (1998) with permission.
Figure 8. Comparison of the effect of measurement and process errors on the estimate of post-recruit abundance. Each solid line is one simulation.
The bottom left boxplot in Figure 9 corresponds to the simulated data in the bottom panel of the previous figure. With increasing standard deviation of process errors, the distribution of $q$ is biased upward. With a standard deviation of 0.5, the dispersion is such that convergence difficulties are encountered. With mixed errors the negative bias from the measurement errors to some extent counteracts the positive bias from the process errors. Adding correlated measurement errors shifts the medians downward as before. The real data probably lie to the right in the upper panel.

What we are really interested in is the distribution of absolute abundance estimates. Table 3 shows the average percent bias and coefficient of variation of legal abundance for combinations of measurement and process errors. The averages are over the 20 years of the data set. With only measurement errors, the bias is low and the CV increases with the standard deviation. With only process errors the bias is increasingly negative, because $q$ was overestimated. With mixed errors the bias is $<5\%$, and this is probably the realm of real data sets.

<table>
<thead>
<tr>
<th>Standard deviation of measurement errors</th>
<th>Standard deviation of process errors</th>
<th>Average % bias of legal abundance</th>
<th>Average CV of legal abundance</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.1</td>
<td>0.0</td>
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</tr>
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<td>12.9</td>
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<td>0.3</td>
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</tr>
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<tr>
<td>0.3</td>
<td>0.3</td>
<td>-3.4</td>
<td>37.0</td>
</tr>
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</table>
Figure 9. Distribution of $q$ relative to known value of 1.0 in Monte Carlo simulations with different magnitudes of both measurement and process error. The explanation of the box plots is the same as for Figure 7. Adapted from Collie & Kruse (1998) with permission.
Bootstrapping the Abundance Estimates

The Kodiak data set (Figure 10) demonstrates the usefulness of catch-survey analysis in situations with no calibrated trawl survey, and therefore no prior estimate of $q$. We performed two runs, one with constant natural mortality ($M$) and one in which $M$ was scaled to anomalies in subsurface temperature in the Gulf of Alaska. Stevens et al. (1994) hypothesized that $M$ is positively related to water temperature. The fit with variable $M$ is improved in the earlier years. Recruitment in 1979 could be considered a measurement-error because post-recruit abundance did not increase the following year.

Finally, we wish to know the bias and dispersion of abundance estimates in each year. This is where the bootstrap comes in. The first pass through DELPOP uses the observed data set (Figure 11). The result of this fit is the input data for the bootstrap. These data are modified with measurement-errors that have the same standard deviation as the observed residuals. The randomization is repeated 200 times and the standard errors of the abundance estimates calculated.

Figure 12 shows the legal abundance and catch of Bristol Bay and Kodiak red king crabs. The dotted line is abundance estimated from the first pass of DELPOP. The dashed line is the bootstrap mean abundance, which is very close to the original estimate. The broken lines are the empirical 95% confidence intervals. For the Kodiak stock, harvest rates increased until 1982, when the fishery collapsed. The fishery has been closed since 1983 and the pot survey discontinued.

Conclusions

Catch-survey analysis is useful for any population that can be classified into recruits and post-recruits and for which catch in numbers is recorded. The measurement-error model provides robust estimates of $q$ and abundance. Of 4,000 Monte Carlo trials, only 25 failed to converge to a solution. Bias is low for realistic levels of process and measurement errors. We can obtain standard errors of the estimates with bootstrapping. Catch-survey analysis is particularly useful for crustacean populations. This method has since been applied to blue crabs and to blue king crab stocks. In addition, we are extending the model to include a pre-recruit stage.
Figure 10. Relative abundances of Kodiak red king crabs measured with a pot survey and estimated with catch-survey analysis. The constant $M$ was 0.36 and the variable $M$s were scaled to ocean temperature anomalies. Adapted from Collie & Kruse (1998) with permission.
Bootstrap Abundance Estimates

Observed Relative Abundance Data

DELPOP Estimation

Estimated Relative Abundance Data

Modify with Random Variability

DELPOP Estimation

Calculate Standard Error of Abundance Estimates

Repeat 200 Times

Figure 11. Flow chart of the sequence of steps in the bootstrap process.
Figure 12. Bootstrap abundance estimates for Bristol Bay and Kodiak red king crabs. Adapted from Collie and Kruse (1998) with permission.
Exercises

1. Perform catch-survey analysis with the method of Collie & Sissenwine (1983) as presented in the chapter. The parameters needed to fit the model are provided in each data file:

- Recruit catchability relative to post-recruit catchability \( \phi \)
- Instantaneous rate of natural mortality \( M \)
- Timing of the commercial catch relative to the survey \( T \)

(a) Use the process-error assumption (linear regression-no intercept) to get an initial estimate of the survey catchability coefficient, \( q \).

(b) Then fit the all observation error model by nonlinear regression. Note that if \( q \) is too large and/or predicted recruits too small, predicted post-recruits could be negative. Use the MAX function to ensure that the predicted post-recruits stay positive, e.g., \( P_t = \text{MAX}(0.001, \text{model prediction}) \).

(c) Plot observed and predicted recruits and observed and predicted post-recruits.

(d) Convert the estimates of recruits and post-recruits from relative numbers to absolute numbers. Calculate the harvest rate and plot it against time. Plot annual catch against time on the same graph.
Species: Yellowtail flounder *Limanda ferruginea*
Location: Georges Bank
Data Source: SAW 24 NMFS fall survey catch per tow*

\[
\begin{align*}
M &= 0.2 \\
T &= 0.5 \\
\phi &= 0.3
\end{align*}
\]

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* The fall trawl survey index was assumed to represent abundance at the start of the next calendar year. Thus the fall 1963 index was moved ahead to 1964, etc. Age 1 recruits would become age 2 and post-recruits would be age 3+.
Species: Atlantic cod  
Location: Georges Bank  
Data source: SAW 24  

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* The fall trawl survey index was assumed to represent abundance at the start of the next calendar year.  
Thus the fall 1963 index was moved ahead to 1964, etc.  
Age-1 recruits would become age 2 and post-recruits would be age 3+
Bibliography


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 $B_{MSY}$.

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 \( \frac{1}{2} K \). The term \( 1 - \frac{B_t}{K} \) 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:

\[
B_{t+1} = B_t + rB_t \left[1 - \left(\frac{B_t}{K}\right)\right] - C_t
\]
(A1) Effect of the intrinsic rate of growth \((r)\) on the stock biomass trajectory \((B_t)\).

Results:

![Graph showing the effect of the intrinsic rate of growth on the stock biomass trajectory](image)

**Figure 1.** Effect of the intrinsic rate of growth \((r)\) on the stock biomass trajectory \((B_t)\).

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:

![Graph showing the effect of the intrinsic rate of growth on the stock biomass growth rate](image)

**Figure 2.** Effect of the intrinsic rate of growth \((r)\) on the stock biomass growth rate \(\left(\frac{dB}{dt}\right)\) 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:

![Graph showing stock biomass trajectory with various initial conditions and catch levels.](image)

**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 $B_0$. 

XII - 4
Increasing catch from 0 to 50 mt over a 50 year period.

Results:

![Graph showing the effect of increasing catch from 0 to 50 mt on the stock biomass trajectory.](image-url)

**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.

Oscillating catch with a 10 year period, and maximum value of 15 mt.

Results:

![Graph showing the effect of an oscillating catch with a period of 10 years and maximum of 15 mt on the stock biomass trajectory.](image-url)

**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 ± 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.

Results:

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 ($B_0$, $r$, $K$) 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 \(B_{MSY}\)).

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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 (B₀) must be selected. A reasonable starting value is 50% of the initial carrying capacity K.

Results:

\begin{align*}
\text{Estimated fishery parameters are:} \\
r &= 0.444 \\
K &= 107.94 \text{ mt} \\
B_{\text{MSY}} &= \frac{K}{2} = 54.4 \text{ mt} \\
\text{MSY} &= r\frac{K}{4} = 11.9 \text{ mt}
\end{align*}

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, $B₀ = 50$ 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 $r$ by 11%. The estimated $B_{\text{MSY}}$ and MSY are 54.4 and 11.9 mt, respectively. The actual $B_{\text{MSY}}$ and MSY are 50 and 12.5 mt, respectively. Thus, the model overestimated $B_{\text{MSY}}$ by 8% and underestimated MSY by 5%.
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.

<table>
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<tr>
<th>Year</th>
<th>Catch</th>
<th>Effort</th>
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<td>60913</td>
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<tr>
<td>1935</td>
<td>72294</td>
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<tr>
<td>1936</td>
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<td>1955</td>
<td>140581</td>
<td>17806</td>
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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.

Results:

![Figure 8. Time-series plot of catch and observed and estimated CPUE.](image)

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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 \( f_{MSY} \) of 32,000 units (class 4 clipper days) (Schaefer 1957). More complex non-equilibrium dynamic biomass models estimate MSY at 110,000 units and \( f_{MSY} \) at 20,000 units (Haddon 2001). The simple model presented here underestimates both MSY and \( f_{MSY} \) by approximately 30% as compared to the more complex dynamic biomass models. However, both the simple and more complex non-equilibrium dynamic biomass models result in more conservative values of MSY and \( f_{MSY} \) compared to the equilibrium model. That is the equilibrium model overestimates both MSY and \( f_{MSY} \) by more than 150%.
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.

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(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?
Bibliography


A REVIEW OF FISH STOCK ASSESSMENT DATA AND MODELS AND THE RESULTING BIOLOGICAL REFERENCE POINTS USED IN FISHERIES MANAGEMENT

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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 sequential population analysis. The data requirements of the models also vary from simple to complex. The output of the models provide both understanding of fish stock dynamics, and reference points that are used in fisheries management.

Reference points used in fisheries management 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 fishing catch-per-unit of effort (CPUE) data can both be used to provide a time history or index of relative stock abundance (Figure 1).

![Figure 1. Indices of relative abundance based on survey and fishery data.](image)

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 to errors in landings or fishery effort data, and changes in survey data collection protocol.

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 $Y_{\text{MAX}}$, $F_{\text{MAX}}$, and $F_{0.1}$.

$Y_{\text{MAX}}$ 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.

$F_{\text{MAX}}$ is the fishing mortality rate that provides $Y_{\text{MAX}}$, 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 $F_{\text{MAX}}$ 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 colloraries 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 the dependent variable as a percentage 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).
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. The percentage chosen should allow sufficient recruitment to ensure sustainability 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 \(F_{x\%}\) of 10, 20, or 30 indicates that there will not be sufficient spawning biomass available for future reproduction, leading to recruitment failure.

**Surplus Production Models**

Surplus production models utilize data on catch (yield), stock abundance, and fishing effort or mortality to determine the maximum sustainable yield at particular levels of stock abundance and fishing effort or mortality. The models are conceptually simple, but are based on assumed equilibrium conditions for the stock that may not exist. The models 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 from survey data or the results of other stock assessment models, and provide both target and limit/threshold of reference points.
MSY is the maximum sustainable yield from the stock under existing conditions.

$B_{\text{MAX}}$ is the virgin biomass of the stock at carrying capacity under existing conditions.

$B_{\text{MSY}}$ is the population size that provides MSY. Using the Schaefer surplus production model, $B_{\text{MSY}}$ is $\frac{1}{2}$ the virgin biomass.

$B_{\text{MSY}}$ is regarded as a limit or threshold reference point representing the minimum acceptable population level for a managed stock. A target biomass level is greater than $B_{\text{MSY}}$.

Another representation of the surplus production model is the catch-fishing mortality or effort function, where yield is related to the effort required to produce that yield or the fishing mortality estimated from catch curve analysis or a VPA (Figure 5).
Figure 5. Catch-fishing effort model showing MSY and $F_{\text{MSY}}$.

MSY is the maximum sustainable yield from the stock under existing conditions. $f_{\text{MSY}}$ or $F_{\text{MSY}}$ is the fishing effort or mortality required to produce MSY.

$f_{2/3\text{MSY}}$ or $F_{2/3\text{MSY}}$ is 2/3 of $f_{\text{MSY}}$ or $F_{\text{MSY}}$. These are important reference points because they provide a substantial decrease in effort or fishing mortality but result in 90+% of the MSY.

$f_{\text{MSY}}$ or $F_{\text{MSY}}$ is now considered a limit reference point, while $F_{2/3\text{MSY}}$ is a target reference point. Fishing at levels greater than $f_{\text{MSY}}$ or $F_{\text{MSY}}$ results in generalized overfishing.

Finally, the surplus-production model 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).
MSY is the maximum sustainable yield from the stock under existing conditions.

MEY is the maximum economic yield attained, and is determined as the largest positive difference between revenue and cost (i.e. where profits are maximized).

$f_{MEY}$ and $F_{MEY}$ are levels of fishing effort and fishing mortality that produce MEY.

Note that when costs exceed revenue due to excessive effort, the fishery ceases to be profitable, and operates at a loss.

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).
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 $B_{MSR}$, 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. These models also provide data for other fishery stock assessment models including stock-recruitment and surplus production models. Age and length structured models offer no specific biological reference points.
Integrating Models

Spawning stock per recruit (SPR) and stock-recruitment (S-R) models can be integrated to provide insight the stock dynamics and biological reference points (Figure 8).

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 $F_{\text{MED}}$ or $F_{\text{REP}}$ 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 ($F_{\text{MED}}$) that results in an average survival ratio (S/R) = 1, at which the stock replaces itself. Other related biological reference points are $F_{\text{LOW}}$ and $F_{\text{HIGH}}$ 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. $F_{\text{LOW}}$ indicates a low probability of stock decline, and some likelihood of stock increase. $F_{\text{HIGH}}$ indicates a high probability that fishing at this level will result in stock declines.

Surplus production and YPR models with their related 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 $B_{MSY}$ and fishing mortality rates relative to $F_{MSY}$.](image)

Optimum yield from a fishery stock will be sustainably achieved when existing biomass exceeds $B_{MSY}$ ($B/B_{MSY} \geq 1$) and when fishing mortality is less than $F_{MSY}$ ($F/F_{MSY} \leq 1$).
Bibliography


