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Incorporating Time-Varying Catchability into Population Dynamic Stock Assessment Models

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Catchability is an important parameter in many stock assessment models because it relates an index of abundance to stock size. We review the theory and evidence for time-varying catchability, its effects on stock assessment estimates, and methods to include time-varying catchability in stock assessments. Numerous studies provide strong evidence that time-varying catchability is common in most fisheries and many fishery-independent surveys and can be caused by anthropogenic, environmental, biological, and management processes. Trends in catchability over time can cause biased estimates of stock size and fishing mortality rates in stock assessment models that do not compensate for them. Methods that use descriptive and functional relationships have been developed to incorporate time-varying catchability in stock assessment models. We recommend that the default assumption for stock assessments should be that catchability varies over time and that multiple methods of including time-varying catchability should be applied. Additional studies are needed to determine relative performance of alternative methods and to develop methods for selecting among models.

Keywords index of abundance, relative abundance, catch per unit effort, catch rate, density-dependent catchability

INTRODUCTION

Catch per unit effort (CPUE) from fishery-dependent or -independent sources is commonly assumed to be proportional to population size, $CPUE \propto N$, and used as an index of abundance in many stock assessments (Quinn and Deriso, 1999). Catchability, the proportionality constant between an index of abundance and population size, is an important parameter in many stock assessment models because it relates an index of abundance to stock size (Hilborn and Walters, 1992; Arreguín-Sánchez, 1996; Quinn and Deriso, 1999). When fishing occurs over a short period (i.e., Ricker (1940) Type I fishery),

$$\frac{C}{E} = qN,$$

where q is catchability, C is catch, and E is effort (Ricker, 1975). In this case, catchability is the proportion of the population caught with one unit of effort. Effort can have many meanings depending on the characteristics of the fishery. This standard usage implicitly assumes that catchability is either constant over time or that it varies around a constant mean (Quinn and Deriso, 1999).

Catchability can also be defined as the proportionality constant between fishing effort and fishing mortality. Based on the Baranov catch equation, $C = F\bar{N}$, for continuous constant fishing and natural mortality over a year (i.e., Ricker (1940) Type II fishery),

$$\frac{C}{E} = q\bar{N},$$

where $\bar{N} = \frac{(1-e^{-Z})}{Z}N$, N is abundance at the start of the year, F is the instantaneous fishing mortality rate, Z is the instantaneous total mortality rate, and $\bar{N}$ is the time-average abundance over the year (Ricker, 1975). An alternative definition

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for catchability as the constant of proportionality between effort and fishing mortality is $C = qEN$. This equation applies when fishing occurs during a period when natural mortality is negligible and changes the units of fishing mortality to per fishing season (Hilborn and Walters, 1992). Such definitions have a long history and may be traced as far back as Baranov in 1916 (Radovich, 1976). Indeed, catchability has been described by some as the most important parameter in stock assessment models (Arreguín-Sánchez, 1996) and is estimated in almost all standard assessment models that estimate absolute abundance (Quinn and Deriso, 1999).

Time-varying catchability is common and should be expected in most fisheries (Winters and Wheeler, 1985) and in many fishery-independent surveys (Walters and Martell, 2004). Anthropogenic, environmental, biological, and management processes may drive changes in catchability over time (Hannesson, 1983; Robins et al., 1998; Skjold et al., 1996). Indeed, there are numerous studies which provide strong evidence that catchability does vary over time (Table 1). CPUE is often proportional to local density. Thus, the local area relative to the area of the entire stock must be considered. This localized effect of the CPUE relationship with density is often called availability (Widrig, 1954; Ricker, 1975).

If time-varying catchability is not allowed for, stock assessments may produce biased estimates (Pope and Shepherd, 1985; NRC, 1998; Wilberg and Bence, 2006) and retrospective patterns as a result (Mohn, 1999). Increases in catchability over time, or when stock sizes are low, can lead analysts to produce overly optimistic estimates of stock size and stock productivity if the change in catchability is not recognized; the resulting overfishing can cause stock collapse (Patterson et al., 1993; Pitcher, 1995; Shertzer and Prager, 2007). Simulation studies indicate that time-varying catchability can cause biomass to be overestimated by more than 100% and fishing mortality to be underestimated by a similar amount (Pope and Shepherd, 1985; Patterson and Kirkwood, 1995; Wilberg and Bence, 2006). The positive bias in biomass in these studies arises because data sets were simulated with increasing trends in catchability. The direction and amount of bias will depend on the pattern and magnitude of catchability changes, amount of fishing mortality, amount and quality of other data, and the type of estimation model (Pope and Shepherd, 1985; Patterson and Kirkwood, 1995; Wilberg and Bence, 2006). Given the critical role that catchability plays in stock assessments, and the fact that catchability likely varies over time, robust methods to incorporate time-varying catchability must be developed, evaluated as to their performance, and regularly applied.

A number of methods have been developed to incorporate time-varying catchability into stock assessments. Despite this, most assessments still use methods that perform poorly when catchability has a trend over time, and relatively few studies have compared the performance of alternative methods when catchability has changed over time (e.g., Pope and Shepherd, 1985; NRC, 1998; Patterson and Kirkwood, 1995; Wilberg and Bence, 2006; Chen et al., 2008).

We are at a crossroads regarding this issue. Fisheries scientists, and most importantly, stock assessment practitioners must understand that (1) ecological theory and a large body of evidence suggests that time-varying catchability is a common phenomenon, (2) failing to incorporate time-varying catchability into stock assessments may produce biased results, (3) multiple methods to incorporate time-varying catchability exist, and (4) additional studies are needed to compare the performance of alternate methods and to develop new and improved methods to incorporate time-varying catchability. The purpose of this article is to thoroughly review potential causes of and evidence for time-varying catchability for individual stocks and provide the information required to bring today's fisheries and stock assessment scientists current with regards to this issue.

CAUSES OF TIME-VARYING CATCHABILITY

Catchability does not represent a single process, but rather a complex set of interactions between fish and fishers (Walters and Martell, 2004). Many causes of time-varying catchability have been identified, and time-varying catchability has been documented in a wide range of fisheries and research surveys, spanning commercial and recreational fisheries, freshwater and marine systems, pelagic and demersal species, fisheries for finfish and shellfish, and research surveys that use passive or active gears (Table 1). In some cases, catchability may change with abundance or the area inhabited by a stock (e.g., Peterman and Steer, 1981; Winters and Wheeler, 1985; Harley et al., 2001), environmental effects (e.g., Green, 1967; Evans et al., 1997; Ziegler et al., 2003), due to changes in fisher behavior or gear (e.g., Hilborn and Walters, 1992), or because of changes in management regulations (e.g., Muller et al., 1997; van Oostenbrugge et al., 2008; Oliveira et al., 2009). Changes in catchability can affect both fishery-dependent and fishery-independent data sources. Catchability change is especially likely when the fishery or survey from which an index of abundance is derived does not cover the full area of the stock (Walters, 2003), although a variety of other causes may also contribute (Pennington and Godø, 1995; Godø et al., 1999).

Fishing Technology, Behavior, or Regulation Changes

It is well known that changes in fishing practices and technology can lead to trends in catchability over time (Garrod, 1964; Gulland, 1964; Kimura, 1981; Hilborn and Walters, 1992; Squires, 1992). Additionally, changes in regulations (Muller et al., 1997), retention of skilled fishermen over time or across generations (Tingley et al., 2005), and learning by fishermen (Walters and Maguire, 1996; Salthaug, 2001) can have substantial effects on catchability. Increasing trends of 2–7% per year in fishing efficiency have been found in economic analyses after compensating for other factors (Hannesson, 1983; Skjold

Table 1 Studies documenting time-varying catchability

Authors	Species (scientific name); location	Category
	Time-varying methods	
Robins et al. (1998)	Australian tiger prawn (*Penaeus esculentus*)	C, D, Sh, M
Ye and Mohammed (1999)	Green tiger prawn (*Penaeus semisulcatus*); Kuwait	C, D, Sh, M
	Density dependence	
Abramson and Tomlinson (1972)	Ocean shrimp (*Pandulus jordani*); California coast	C, D, Sh, M
Schaaf and Huntsman (1972)	Atlantic Menhaden (*Brevoortia tyrannus*); U.S. Atlantic coast	C, P, F, M
Schaaf (1975)	Atlantic Menhaden (*Brevoortia tyrannus*); U.S. Atlantic coast	C, P, F, M
Pope and Garrod (1975)	Cod (*Gadus morhua*); Barents Sea and north Atlantic	C, D, F, M
MacCall (1976)	Pacific sardine (*Sardinops sagax*); 1937–1944 Eastern Pacific Ocean	C, P, F, M
Ulltang (1976)	Atlanto-Scandinavian herring (*Clupea harengus harengus*); Norway	C, P, F, M
Peterman (1980)	Chinook salmon (*Oncorhynchus tshawytscha*); Oregon and British Columbia	A, An, F
Schaaf (1980)	Atlantic Menhaden (*Brevoortia tyrannus*); U.S. Atlantic coast	C, P, F, M
Houghton and Flatman (1981)	Cod, (*Gadus mohua*); west-central North Sea	C, D, F, M
Peterman and Steer (1981)	Chinook salmon (*Oncorhynchus tshawytscha*); Oregon and British Columbia	R, An, F
Henderson et al. (1983)	Lake whitefish (*Coregonus clupeaformis*); Lake Huron	C, D, F, Fr
Crecco and Savoy (1985)	American shad (*Alosa saidissima*); Connecticut River	C, An, F
Winters and Wheeler (1985)	Atlantic herring (*Clupea harengus harengus*);	C, P, F, M
Ralston et al. (1986)	Bottom fishes (lutjanids, serranids, and carangids); Johnston Atoll	R, D, F, M
Richards and Schnute (1986)	Quillback rockfish (*Sebastes malinger*); Strait of Georgia, British Columbia	R, D, F, M
Deriso and Parma (1987)	Snappers (*Pristipomoides zonatus, P. auricilla,* and *Etelis carbunculus*); Mariana Islands, Pacific Ocean	S, D, F, M
Richards (1987)	Pacific rockfishes (*Sebastes* spp.); Strait of Georgia, British Columbia	R, D, F, M
Csirke (1989)	Peruvian anchoveta (*Engraulis ringens*); Peru	C, P, F, M
Crecco and Overholtz (1990)	Georges Bank haddock (*Melanogrammus aeglefinus*); Georges Bank	C, D, F, M
Gordoa and Hightower (1991)	Cape Hake (*Merluccius capensis*); coasts of Angola and Namibia	C, P, F, M
Rose and Leggett (1991)	Atlantic cod (*Gadus morhua)*; Northwest Atlantic Ocean	C, D, F, M
Shardlow (1993)	Pacific salmon (*Oncorynchus* spp.); Strait of Georgia, British Columbia	R, An, F
Hutchings and Meyers (1994)	Atlantic cod (*Gadus morhua*); Northwest Atlantic Ocean	C, D, F, M
Swain et al. (1994)	Atlantic cod (*Gadus morjua*); Gulf of St. Lawrence	S, D, F, M
Hannah (1995)	Ocean shrimp (*Pandalus jordani*); California	C, D, Sh, M
Shuter et al. (1998)	Lake trout (*Salvelinus namaycush*); Ontario lakes	R, D, F, Fr
Hansen et al. (1998)	Lake trout (*Salvelinus namaycush*); Lake Superior	S, D, F, Fr
Godø et al. (1999)	Cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinis*), and American plaice (*Hippoglossoides platessoides*); Barents Sea and northwest Atlantic	C, D, F, M
Rose and Kulka (1999)	Northern cod (*Gadus morhua*); Northwest Atlantic Ocean	C, D, F, M
Hansen et al. (2000)	Walleye (*Sander vitreus*); Northern Wisconsin lakes	C, R, D, F, Fr
Harley et al. (2001)	ICES cod, flatfish, and gadiformes	C, D, F, M
Pérez and Defeo (2003)	Nylon shrimp (*Heterocarpus reedi*); Chilean coast	C, D, Sh, M
Rodgers et al. (2003)	Walleye (*Sander vitreus*); Northern Wisconsin lakes	S, D, F, Fr
Hansen et al. (2004)	Walleye (*Sander vitreus*); Northern Wisconsin lakes	S, D, F, Fr
Pérez and Chávez (2004)	Surf clam (*Mesodesma donacium*); Coquimbo Bay, Chile	A, D, Sh, M
Hansen et al. (2005)	Walleye (*Sander vitreus*); Northern Wisconsin lakes	C, R, D, F, Fr
Jiao et al. (2006)	Yellow perch (*Perca flavescens*); Lake Erie	R, C, D, F, Fr
Zhou et al. (2007)	Banana prawn (*Penaeus merguiensis*); Gulf of Carpentaria, Australia	C, D, Sh, M
Rindorf and Andersen (2008)	North Sea cod (*Gadus morhua*); North Sea	C, D, F, M
	Effort dependence	
Fonteneau and Richard (2003)	Tunas and billfishes; Indian Ocean	C, P, F, M
Salthaug and Aanes (2003)	Northeast Arctic cod (*Gadus morhua*), northeast Arctic haddock (*Melanogrammus aeglefinus*) and saithe (*Pollachius virens*)	C, D, F, M
van Oostenbrugge et al. (2008)	Plaice and sole; Dutch beam trawl fishery	C, D, F, M
	Environmental methods	
McLeese and Wilder (1958)	American lobster (*Homarus americanus*); northwestern Atlantic	R, D, Sh, M
Paloheimo (1963)	American lobster (*Homarus americanus*); northwestern Atlantic	C, D, Sh, M
Green (1967)	Yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Euthynnus pelamis*); Eastern Pacific Ocean	C, P, F, M
Rose and Leggett (1989)	Atlantic cod (*Gadus morhua*); northern Gulf of St. Lawrence	C, D, F, M
Evans et al. (1997)	Banana prawns (*Panaeus merguiensis*); Gulf of Papua	C, D, Sh, M
Swain et al. (2000)	Atlantic cod (*Gadus morhua*); Gulf of St. Lawrence	C, P, F, M
Ziegler et al. (2003)	Southern rock lobster (*Janus edwardsii*); Tasmania, 1992–1999	C, D, Sh, M
	Multiple causes	
Bannerot and Austin (1983)	Yellowtail snapper (*Ocyurus chrysurus*); Florida	R, D, F, M
Hannesson (1983)	Lofoten cod (*Gadus morhua*)	C, D, F, M

(Continued on next page)

Table 1 Studies documenting time-varying catchability (Continued)

Authors	Species (scientific name); location	Category
Angelsen and Olsen (1987)	Lofoten cod (*Gadus morhua*)	C, D, F, M
Squires (1992)	U.S. Pacific coast multi-species trawl fishery	C, D, F, M
Patterson et al. (1993)	Chub mackerel (*Scomber japonicus*); eastern central Pacific	C, P, F, M
Skjold et al. (1996)	Norwegian cod (*Gadus morhua*)	C, D, F, M
McInerny and Cross (2000)	Largemouth bass (*Micropterus salmoides*); Minnesota lakes	S, D, F, Fr
Hannesson et al. (2008)	Lofoten cod (*Gadus morhua*)	C, D, F, M
Ye and Dennis (2009)	Torres Straight rock lobster (*Panulirus ornatus*)	C, D, Sh, M

Categories represent fishery or stock characteristics: C—commercial fishery; R—Recreational fishery; S—research survey; A—artisanal fishery; P—pelagic species; D—demersal species, An—anadramous species; F—finfish; Sh—shellfish; M—marine; Fr—freshwater.

et al., 1996; Robins et al., 1998; Hannesson, 2007). Such changes include bigger motors and boats, which allow new fish aggregations to be exploited, as well as sonar and GPS plotters, which allow fishermen to accurately target productive habitats and aggregations (Hannesson, 1983; Robins et al., 1998; Skjold et al., 1996). Recent assessment reports for the U.S. Gulf of Mexico and south Atlantic fisheries management regions have hypothesized that navigational aids (i.e., global positioning systems (GPS) and GPS plotters), motor size, and captain experience may have caused a 35% increase in catchability since the 1980s (Southeast Data Assessment and Review (SEDAR), 2006). Increased deployment of fish aggregation devices, as well as changes in bottom habitat can cause changes in distribution and fish densities with accompanying changes in catchability (Arreguín-Sánchez, 1996). Fishermen may change their targeting preferences to maximize profits as market prices, fishing costs, and CPUE change (Hutchings and Myers, 1994; Salthaug and Aanes, 2003). These economic changes may also drive changes in the dynamics of exploited fish populations that can lead to increases or decreases in catchability (Hannesson, 1983).

Management and regulations can have a significant effect on catchability, and often managers will implement regulations with the intent of reducing catchability (Oliveira et al., 2009). Changes in size, bag, or trip limits can cause sudden changes in catchability by redefining acceptable catch, forcing fishermen to discard (and hence not record) a portion of previously retained catch (Gillis et al., 1995; Fare et al., 2006; SEDAR, 2006). Temporal and spatial regulations may affect catchability by redistributing fishermen away from optimal times or fishing grounds or towards spatial boundaries where fish densities are increased (McGilliard and Hilborn, 2008). Seasonal or spatial closures can also affect catchability because catchability can change seasonally (Skjold et al., 1996; Ye and Mohammed, 1999) and differ among areas (Walters, 2003). Finally, fishery managers may choose to regulate or promote changes in fishing gears used by commercial or recreational fishermen. Such changes include the shift from J-hooks to circle-hooks, which has caused increases in CPUE for billfish, pelagic longlines, and Gulf of Mexico longlines (Hoey, 1996; Falterman and Graves, 2002; Prince et al., 2002).

Table 2 Variable names

Variable name	Definition
N	Total biomass
SSB	Spawning stock biomass
C	Catch
CPUE	Catch-per-unit-effort
D	Local density
HB	Harvestable biomass
R	Spatial patchiness of effort
SE	Spatial extent of effort
SA	Stock area
t	Time in years
S	Time in seasonal units
E	Nominal fishing effort

Fisher behavior, in terms of where and when fishermen choose to fish, can cause catchability to vary over time (Gillis and Peterman, 1998). Additional units of effort added to a fishery can have lower catchability than previous units of effort (van Oostenbrugge et al., 2008), which we term effort dependent catchability. This phenomenon can be caused by gear competition, selection of suboptimal fishing locations after better ones are fully fished, or localized depletion in areas that are heavily fished (Ricker, 1975). Effort dependent catchability has been found in several fisheries for a range of species (e.g., Muller et al., 1997, Fonteneau and Richard, 2003; van Oostenbrugge et al., 2008).

Density Dependence

Paloheimo and Dickie (1964) suggested that catchability would be density dependent when a stock is contagiously distributed and searching by fishermen is non-random, although gear saturation can also lead to this phenomenon (Ricker, 1975; Richards and Schnute, 1986). Density-dependent catchability has been reviewed in Winters and Wheeler (1985) and Arreguín-Sánchez (1996) and has been extensively documented in a variety of species and regions (Table 1). The typical pattern for density-dependent catchability is that catchability increases as abundance declines, thus causing fishery CPUE to be "hyperstable," where CPUE remains high despite decreases in abundance (Figure 1; Hilborn and Walters, 1992). Hyperstable CPUE in combination with a stock assessment model that does not account for it can cause underestimation of abundance

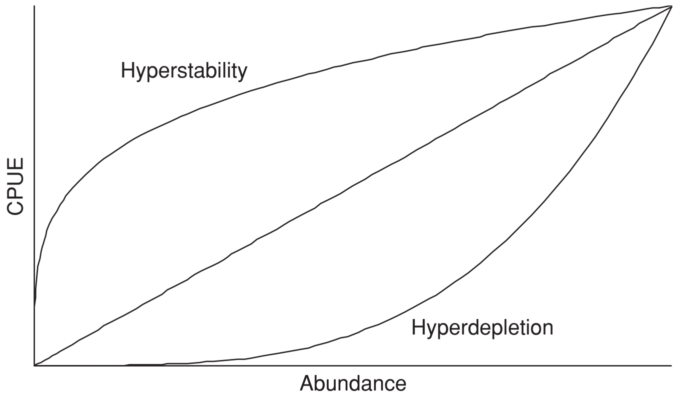

Figure 1 Potential patterns of density-dependent catchability on catch per unit effort (CPUE). Reproduced from Hilborn and Walters (1992) with kind permission of Springer Science and Business Media.

changes and lead to misinterpretation of stock collapse or recovery (NRC, 1998). It may also lead to catchability-led stock collapse, where density-dependent catchability leads to disequilibrium between fisher and stock behavior in a fishery where total catch is not controlled (Pitcher, 1995; Mackinson et al., 1997).

The typical model used for density-dependent catchability is a power function of density (Paloheimo and Dickie, 1964; Table 2; Table 3; Eq. 3.1). If the exponent parameter is greater than zero, catchability exhibits hyperdepletion where CPUE changes more rapidly than stock size; if the exponent parameter is zero, catchability is constant and CPUE is proportional to stock size; if the exponent is negative, CPUE will show hyperstability and CPUE decreases less rapidly than stock size (Figure 1). Many generalizations have also been proposed, including effort and density dependence (Eq. 3.2; Hannesson, 1983), spatial density dependence (Eq. 3.3; Salthaug and Aanes, 2003), or generalized density dependence to accommodate refuges (Eq. 3.4; Richards and Schnute, 1986).

Much of density-dependent catchability can be thought of as an overlap between fishermen (or scientists) and the stock. Because CPUE is often an index of local density, it reflects abundance where fishing takes place. Thus, how the distribution of a stock changes spatially as its abundance changes can affect catchability in fisheries and surveys. In order for CPUE from a restricted part of a stock's range to be a reliable index of abundance, the stock must decrease in the same proportion across the entire range in which it is fished (Figure 2). If fishing (or a research survey) only takes place in a small part of the range of a stock and stock density changes in some locations are not proportional to overall abundance, CPUE can exhibit hyperstability or hyperdepletion (Fréon and Misund, 1999). Range contraction of some stocks has been extensively documented (MacCall, 1990; Rose and Kulka, 1999) and is supported by basic models of habitat use (MacCall, 1990). Research surveys and localized fisheries that only cover a small portion of the stock's range may be particularly vulnerable to this cause of change in catchability. Walters (2003) described how hyperdepletion could occur when a fishery is expanding spatially and is able to initially target areas of high abundance. Density-dependent effects may vary between different temporal scales (Rose and Leggett, 1991; Atran and Loesch, 1995), spatial scales (Prince and Hilborn, 1998), and degrees of data aggregation (Bannerot and Austin, 1983). This same effect can also occur at a smaller scale if a stock preferentially uses habitat that is not surveyed.

Table 3 Methods for describing patterns of time-varying catchability and including time-varying catchability in assessment models

Equation number	Method	Function
Mechanistic		
3.1	Density-dependent	$q_t = \alpha N_t^{\beta}$
3.2	Density-dependent	$q = \frac{a}{1+bN}$
3.3	Effort and density (derived from Cobbs-Douglas catch equation)	$CPUE_t = \alpha E_t^{\gamma} N_t^{\beta}$
3.4	Density dependence and refugia	$q_t = \alpha N_t^{\beta} - c$
3.5	Spatial data (R is spatial patchiness of effort; D is spatial extent of fishing fleet of effort)	$q_t = \alpha - \beta D$ $q_t = \alpha - \beta R$
3.6	Density dependence with refugia and catch rate saturation	$CPUE = \frac{p+qD}{1+rD}$ if $D > -p/q$; $CPUE = 0$ if $D \leq -p/q$
3.7	Environmental variables	$q_t = f(V_t)$
Descriptive		
3.8	Step function of time	$q_t = \begin{cases} q_1 & \text{for } t < t_1 \\ q_2 & \text{for } t_1 \leq t < t_2 \\ \vdots & \\ q_n & \text{for } t_n \leq t \end{cases}$
3.9	Polynomial of time	$q_t = \beta_0 + \beta_1 t + \beta_2 t^2 + \ldots + \beta_n t^n$
3.10	White noise (log-scale)	$q_t = \bar{q} e^{\varepsilon_t}$
3.11	Random walk (log-scale)	$q_{t+1} = q_t e^{\varepsilon_t}$

Models are separated into mechanistic (based on functional relationships) or descriptive (allow changes over time without specifying mechanisms) categories.

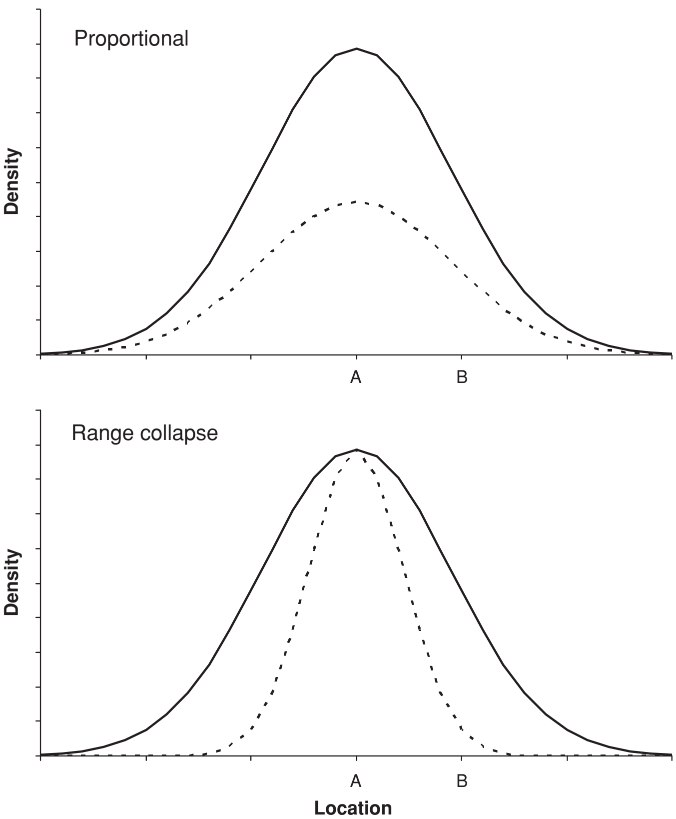

Figure 2 Potential effects of a decrease in abundance on the density of a stock. The upper panel indicates proportional change in density across the entire range, and the lower panel indicates a contraction of the range with decreasing abundance. Locations A and B indicate potential sites where catch-per-unit-effort could be measured. The estimated change in relative abundance would be different at each site, but the overall change for the whole stock is the same in both cases. In the upper panel, the proportional change at sites A and B would be equivalent. In the lower panel, site A would display hyperstability and site B would display hyperdepletion.

For example, a species that preferentially uses rocky habitat may exhibit density-dependent catchability in a trawl survey that only covers areas with little structure (Swain et al., 1994).

Evidence of density-dependent catchability has been observed in a wide range of fisheries, and many studies attribute this pattern to the ability of fishermen to target dense aggregations. The collapse of the north Atlantic cod (*Gadus morhua*) fishery is partly attributed to a damped decrease in CPUE as abundance fell (Hutchings and Myers, 1994; Walters and Maguire, 1996; Shelton and Lilly, 2000), and CPUE even increased in some locations as cod stocks declined (Rose and Kulka, 1999). Density-dependent catchability has been observed in the commercial purse seine fishery for Atlantic menhaden, where catchability increased as abundance decreased (*Brevoortia tyrannus*; Schaaf and Huntsman, 1972; Schaaf, 1975, 1980). Peterman and Steer (1981) also found that catchability in recreational fisheries for Chinook salmon (*Onchorynchus tschawytscha*) increased with decreasing abundance, and Harley et al. (2001) found hyperstable catchability in a meta-analysis of International Council for Exploration of the Sea (ICES) commercial fisheries. Bannerot and Austin (1983) found hyperstable catchability in a recreational headboat fishery. Fonteneau and Richard (2003) found evidence of hyperdepletion in longline fisheries in the Indian Ocean.

Evidence of density-dependent catchability has also been found in fishery-independent surveys that use active and passive gears. Godø et al. (1999) found that catchability of research trawls for cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinis*), and American plaice (*Hippoglossoides platessoides*) tended to increase with density (hyperdepletion) because fish behavior upon encountering the net differs with fish density. Swain et al. (1994) suggested that density-dependent catchability (hyperdepletion) in a fishery-independent trawl survey for Atlantic cod was caused by changes in the spatial distribution of the stock relative to the survey area, which could be caused by preferential use of untrawlable habitat at low abundance. Rodgers et al. (2003) found that catchability of walleyes (*Sander vitreus*) was hyperstable in electrofishing and fyke net surveys in northern Wisconsin lakes, and McInerny and Cross (2000) found that catchability of largemouth bass (*Micropterus salmoides*) in an electrofishing survey was hyperstable. Gill net surveys for lake trout (*Salvelinus namaycush*) in Lake Superior were also found to exhibit hyperstable density-dependent catchability caused by gear saturation (Hansen et al., 1998).

Several studies have tested the hypothesis that catchability is density dependent, but were unable to reject the null hypothesis. Beard et al. (1997), Hansen et al. (2000), and Newby et al. (2000) failed to reject the null hypothesis that catch rates of walleyes in a recreational angling fishery were proportional to abundance, although Hansen et al. (2005) later found that catchability of walleyes was density dependent in an analysis that included measurement error in abundance estimates. Fournier (1983) tested the hypothesis that fishery catchability was density dependent in a stock assessment of Pacific cod (*Gadus macrocephalus*), but the analysis failed to reject the null hypothesis that catchability was constant. Richards and Schnute (1986) and Richards (1987) found that CPUE was proportional to density for research angling for several rockfish (*Sebastes spp.*) species individually, but not as a group.

Environment

Environmental change can affect fish and fisher behavior, and thus affect catchability of fishery-dependent and -independent indices of abundance. Changes in fish behavior may occur seasonally or across years due to a variety of changing hormonal and environmental cues or natural and artificial pressures. When these changes affect feeding habits or fish densities, they can cause seasonal or continuous changes in catchability (Skjold et al., 1996; Soldmundsson et al., 2003). Oceanographic changes or cycles may cause concentrations or dispersal of fish, as in the Peruvian anchoveta fishery (Csirke, 1989; Hilborn and Walters, 1992). Reduced catchability of green tiger prawns (*Panaeus semisulcatus*) is associated with low temperatures (Ye and

Mohammed, 1999), while catchability of purse-seines for tuna decreases as depth of the thermocline increases (Green, 1967). Evans et al. (1997) found that catchability of prawns (*Panaeus merguiensis*) is affected by rainfall. Climate change scenarios may cause trends in catchability through behavioral changes (Ye and Mohammed, 1999) or changes in spatial distribution. These types of changes may become particularly problematic for research surveys if catchability of stocks of interest is affected by global climate change.

Combinations of Factors

Because of the many potential causes of time-varying catchability, multiple mechanisms will often act in a fishery, and the overall effect will be difficult to predict *a priori*. For example, catchability decreased overall for yellow perch (*Perca flavescens*) in Lake Michigan in a recreational angling fishery (Figure 3). This change in catchability was likely due to combined effects of management, changes in abundance, and changes in the environment. Ziegler et al. (2003) found that catchability was influenced by physiological processes, water temperature, and density-dependent (hyperstable) processes for Tasmanian rock lobsters (*Jasus edwardsii*). Ye and Mohammed (1999) found that catchability was associated with schooling behavior, water temperature, and increased with abundance for green tiger prawns. Patterson et al. (1993) found that catchability was positively related with abundance and negatively with sea surface temperature and sea surface level for chub mackerel (*Scomber japonicus*).

Economic methods have been developed to estimate how factors, such as catchability, stock abundance, and nominal fishing effort, affect fishery production (Squires, 1992; Andersen 2005). In one such method, trends in catchability (commonly called fishing efficiency) are estimated as trends in "total factor productivity," factors that affect output (i.e., catch) other than inputs (i.e., effort). Studies using these methods have generally demonstrated strong density dependence and increasing residual trends in catchability over time (Hannesson, 1983; Squires, 1992; Skjold, 1996; Hannesson, 2007). Total factor productivity may in turn be decomposed as technical changes and efficiency changes (Oliveira et al., 2009). Other multiple factor studies have attempted to estimate trends in catchability using other methods (Tingley et al., 2005). These studies link residuals in CPUE (after compensating for density dependence and effort dependence) to vessel-specific or fishery-wide factors. These kinds of analyses may provide a useful avenue in the future for estimating catchability changes due to a variety of management, gear, technical, and environmental changes (Fare et al., 2006).

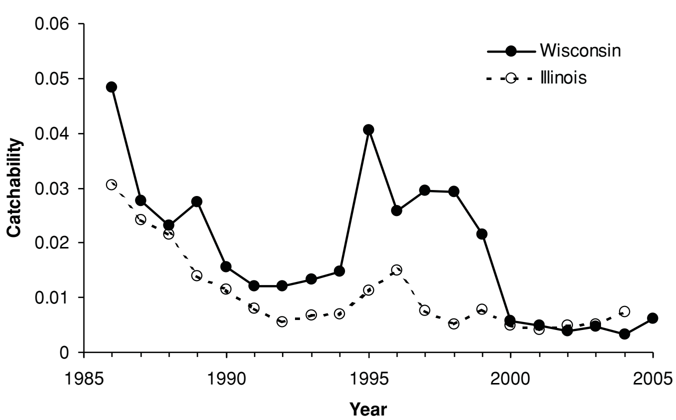

Figure 3 Changes in catchability over time for recreational fisheries for yellow perch in Wisconsin and Illinois waters of southern Lake Michigan.

METHODS FOR INCORPORATING TIME-VARYING CATCHABILITY

Methods have been developed to incorporate time-varying catchability in stock assessment models, but there is little consensus about the best practices in this area (e.g., Fox, 1974; Fournier and Archibald, 1982; Fréon, 1988; Prager, 1994; Schnute, 1994; Fournier et al., 1998; Shepherd and Pope, 2002; Walters and Martell, 2004). Several general methods have been developed to "correct" or standardize effort or CPUE data series for time-varying catchability or to allow catchability to vary over time within an assessment model: (1) standardization of indices of abundance, (2) ignoring or down-weighting an index if its catchability is suspected to have changed (NRC, 1998; Francis et al., 2003), (3) modeling catchability as a function of time (e.g., Prager, 1994; Shepherd and Pope, 2002; Walters and Martell, 2004), (4) modeling catchability as a function of density or an environmental variable (e.g., Fox, 1974; Fournier, 1983; Fréon, 1988; Shepherd, 1999), or (5) allowing catchability to change over time using state space models (e.g., Sullivan, 1992; Gudmundson, 1994; Schnute, 1994). State space techniques and modeling catchability as a function of time do not ascribe causation for changes in catchability, while use of functions of density or external variables assumes that the variables used to describe changes are the dominant ones. Here, we focus on methods that could be applied in surplus production models (Prager, 1994), virtual population analysis (VPA) (Shepherd and Pope, 2002), and statistical catch-at-age analysis (SCA) (Fournier and Archibald, 1982; Deriso et al., 1985; Schnute, 1994), although these methods are generally applicable in population dynamics stock assessment models that are statistically fitted.

Standardizing CPUE

Traditionally, standardization of CPUE has been the primary method used to attempt to account for time-varying catchability. Standardizing effort data has a long history in fisheries where fishery effort is adjusted for spatial and temporal patterns, fishery effort or CPUE is adjusted for known changes in fishing efficiency, or effort in other gears is converted to a standard gear in which catchability is not thought to have changed (Beverton and Holt, 1957; Gulland, 1964; Ricker, 1975; Gulland, 1983).

Improvements in vessels, and other fisher behaviors can be accounted for either by analyzing CPUE data to estimate mean CPUE by accounting for vessel characteristics and spatial and temporal patterns of fishing (Gavaris, 1980; Lo et al., 1992; Maunder and Starr, 2003; Maunder and Punt, 2004) or by integrating the standardization process into the stock assessment model (e.g., Maunder, 2001).

Most current single-species assessments attempt to address changes in catchability by "standardizing" CPUE data to minimize changes that might affect catchability, such as fisher targeting, effort changes, and technological changes. Many methods and models have been developed to standardize CPUE data for known changes in times and locations fished and vessel characteristics, although most applications do not evaluate potential interactions with year effects, which complicates interpretation of indices. Models used include general linear models (Gavaris, 1980), generalized linear models, mixed models, and generalized additive models (Maunder and Punt, 2004). However, standardization can only correct for measured factors that affect catchability and require that data are available for each factor. Thus, changes in catchability caused by technological changes in the recreational fishery such as adoption of GPS or sonar and increases in boat length are rarely able to be well described (Squires, 1992).

Additional information, such as stock range area, spatial concentration of effort, and spatial patchiness of effort, have been suggested as covariates in CPUE standardization models to compensate for density dependence or effort dependence (Winters and Wheeler, 1985; Salthaug and Aanes, 2003). Swain and Sinclair (1994) suggest that a ninety-five percent coverage area is the optimal spatial metric for stock range area in such uses. Salthaug and Aanes (2003) suggested using a linear relationship between catchability and spatial concentration of effort to correct CPUE for changes in the spatial distribution of fishing effort. Bannerot and Austin (1983) suggested using a transformation of the proportion of zero catches as an index of abundance for a headboat fishery. Stephens and MacCall (2004) proposed using multi-species logbook data to determine which sets occurred within likely habitat for a species of interest.

While standardization techniques are useful and should be used to correct for known factors affecting catchability, it is unlikely that all the factors that affect catchability can be included in the standardization. Although some gear and regulatory changes may be controlled for during index standardization (Maunder and Punt, 2004), other significant changes may not be recorded in surveys that track changes in fishing gears (Marchall et al., 2007). Therefore, methods to incorporate time-varying catchability in assessment models are often still necessary even when indices have been standardized.

Ignoring CPUE Time Series and Assigning Arbitrary Weights

Choosing among CPUE time series to include in an assessment model can be difficult. In general, fishery-independent indices are often thought to better reflect relative abundance than fishery-dependent indices (NRC, 1998). When good fishery-independent indices are available, use of fishery-dependent indices with their potential problems of time-varying catchability is not necessary. Indeed, based on the results of their simulations, the NRC (1998) recommended that fishery-dependent indices of abundance should be ignored if a fishery-independent index of abundance is available, although many assessments use both fishery-dependent and -independent data if they are available (e.g., Millar and Methot, 2002; Francis et al., 2003; Wilberg et al., 2005). However, fishery-dependent indices may have some benefits over fishery-independent indices because longer time series are often available and they often cover a larger area of the stock than fishery-independent surveys. Simulation studies suggest that using fishery-dependent indices in a stock assessment can improve accuracy of estimates if methods that allow for time-varying catchability are used (Wilberg and Bence, 2006). Ignoring potential indices of abundance requires that more than one index of abundance is available and assumes that problems caused by including an index outweigh the potential benefits.

Assigning arbitrary weights to each index is commonly done when multiple indices of abundance are included in a stock assessment (Francis et al., 2003). Often stock assessment scientists will substantially "down-weight" (i.e., specify an arbitrarily large standard deviation) fishery-dependent CPUE data in an assessment model if a fishery-independent index of abundance is available for a given stock (Francis et al., 2003). This implies that the variance of some indices is specified as larger than other data sources. However, the problem with trending catchability is that errors will be correlated over time and will violate the assumption of independence that is commonly used in assessment models. Therefore, down-weighting indices will often still produce problems that show up as trends in the residuals of fits to some indices of abundance and retrospective patterns in assessment results.

Functions of Density or Environmental Variables

Some researchers have developed methods to explicitly include density-dependent catchability and effects of the environment on catchability in stock assessments (Fox, 1974; Cooke, 1985; Fournier, 1983; Fréon, 1988; Shepherd, 1999; Maunder and Watters, 2003; Chen et al., 2008). The power model used to incorporate density-dependent catchability (Eq. 3.1) into assessments was developed by Paloheimo and Dickie (1964). Although density-dependent catchability has been applied in assessment models in a range of fisheries since the mid 1970s (e.g., MacCall, 1976; Fournier, 1983; Chen et al., 2008), density-dependent catchability does not seem to be commonly incorporated into stock assessments that provide management advice. Other functions for density-dependent catchability are also available (Eqs. 3.2–3.5), but we were unable to find examples of these being used in stock assessments.

Methods to allow effects of the environment on catchability (Eq. 3.6) have also been developed (Fréon, 1988; Methot, 2000; Maunder and Watters, 2003). Fréon (1988) developed a suite of 20 surplus production models that allow for environmental and density-dependent effects on stock productivity and catchability. Maunder and Watters (2003) provided a general framework for allowing parameters to be a function of environmental variables in an SCA. Stockhausen et al. (2006) included the effect of mean bottom temperature on trawl survey catchability in an SCA of flathead sole (*Hippoglossoides elassodon*). Swain et al. (2000) attempted to include bottom temperature in a VPA for Atlantic cod in the southern Gulf of St. Lawrence. They found that the addition of bottom temperature did not improve the fit of the model and suggested that only environmental variables that explain residual variation in the assessment model be used.

Functions of Time

Many authors have suggested attempting to model catchability as a step function (Eq. 3.7) or a polynomial of time (Eq. 3.8; Prager, 1994; Shepherd and Pope, 2002; Walters and Martell, 2004). The parameters of the function are then estimated during the model fitting. Other functions of time, such as cubic splines, could be used to model time-varying parameters (Walters and Martell, 2004), but we were unable to find examples in which this technique was applied. Therefore, we only discuss step functions and polynomials.

Step functions require that time blocks are specified, and separate catchability parameters are estimated for each block. There is a tradeoff between the number of blocks and the estimability of parameters; the longest blocks possible are most desirable in terms of parsimony, but longer blocks limit the amount of change in catchability. If enough blocks are used, this will allow substantial variability in catchability over time, but it may be difficult to estimate parameters for time blocks shorter than five years. As the block size decreases to the length of the time step in the model, this method becomes like estimating a separate catchability for each year (i.e., ignoring CPUE data).

Identifying appropriate blocks of time is often a somewhat arbitrary process. Ideally, blocks should be determined by dominant changes in the fishery or survey that are thought to change catchability. Examples of this could be a substantial change in regulations, such as a seasonal closure when seasonal patterns in catchability exist, or changes made to a survey gear or vessel. In principle, time blocks need not be linked to a specific cause of time-varying catchability. Mohn (1999) found that blocks of time could be used in VPAs to reduce retrospective bias. However, despite causing reductions in retrospective patterns, estimates were often still biased, suggesting that fishery biologists should not base the choice of time blocks on reduction of retrospective pattern alone.

Step functions have been commonly used to model changes in catchability. Prager (1994) suggested using a step function for surplus production models. Simpendorfer et al. (2000) estimated catchability for two periods for their assessment of whiskery shark (*Furgaleus macki*) in southwestern Australia because of a change in target species of the fishery during the time series in an age-structured production model. McAllister and Ianelli (1997) estimated catchability for two periods because of changes in survey gear for yellowfin sole (*Limanda aspera*) in the eastern Bering Sea.

Polynomials of time have been suggested as a general method to allow parameters of assessment models to vary over time (Walters and Martell, 2004). Many authors have suggested modeling catchability as a linear increase and estimating the parameters during model fitting (Prager, 1994; Shepherd and Pope, 2002), but few assessments seem to apply this technique (e.g., Marchal et al., 2003). Polynomials of higher order could also be used, but we were unable to find any examples of these. However, quadratic functions of time were used in a similar application to model parameters of a function for time-varying selectivity for lake whitefish (*Coregonus clupeaformis*) stock assessments in the Great Lakes (Ebener et al., 2005). A potential difficulty with polynomials of time is that the shapes described by lower order polynomials may not be flexible enough to adequately model time-varying catchability. High order polynomials may have too many parameters to estimate, and even short projections may be quite poor.

State Space Methods

State space techniques have been developed and applied in surplus production models (Meyer and Millar, 1999; Punt, 2003), VPAs (Porch, 1999), and SCAs (Gudmundsson, 1994; Schnute, 1994; Fournier et al., 1998) . This is a general approach that allows parameters to vary over time, often without specifying the cause of variation. A state space approach explicitly includes process and observation error in the model (Schnute, 1994). These models usually consist of a state vector, an observation vector, and a control vector. State space models explicitly model the system dynamics as a function of the state vector and the controls, which do not depend on the states. Observations are modeled as a function of the unknown state vector. If models are linear and errors are normal, a Kalman filter can be used to estimate the parameters (e.g., Sullivan, 1992). For nonlinear models, maximum penalized likelihood (i.e., highest posterior density or maximum a posteriori) and Bayesian methods are commonly used to estimate parameters (Schnute, 1994), but other methods are also available (Punt, 2003).

Several methods are commonly used to allow catchability to change over time in a state space framework, although many state space assessments assume constant catchability (e.g., Millar and Meyer, 2000). Most state space stock assessment models with time-varying catchability assume multiplicative independent lognormally distributed errors in catchability (Eq. 3.9; white noise; Fournier and Archibald, 1982; Butterworth et al., 2003). This is equivalent to assuming additive independent normally distributed errors on the log scale. The error variance of catchability is often not easily estimable and other information, such as the ratio of observation to process error (Schnute and Richards, 1995), must be specified. In practice, the variance of the catchability deviations is often specified by the analyst (e.g., Fournier and Archibald, 1982).

Often the variance of the index of abundance in the assessment model is specified as the estimated variance of CPUE. This assumes that the only error is the error in measuring CPUE and that if CPUE was measured exactly, it would be proportional to abundance. This is generally not a good idea because the estimated variance of CPUE will be a lower bound on the possible variance for the index of abundance because it only accounts for the precision of CPUE. The other potential component of error is variation in catchability. Catchability variation would be in addition to precision of CPUE.

Random walks have also been used to model gradual changes in catchability over time (Eq. 3.10). Modeling catchability as a random walk has been widely applied in SCAs (e.g., Fournier et al., 1998; Wilberg et al., 2005), rarely applied in VPAs (e.g., Porch, 1999), or during index standardization (Stockhausen and Fogarty, 2007), and has only been suggested for surplus production models (Smith and Addison, 2003). Many causes of time-varying catchability could lead to gradual changes over time. When random walks are implemented for catchability, the log of catchability is usually the estimated parameter, so that catchability cannot become negative to stabilize estimation procedures, and the variance of the log of catchability is often specified.

Priors and Variance Components of Time-Varying Catchability

For nonlinear models, maximum penalized likelihood (i.e., highest posterior density) and Bayesian methods are commonly used to estimate parameters (Schnute, 1994). The Bayesian approach utilizes Bayes Theorem to obtain the posterior density of the parameter values:

$$p(\theta|y) \propto p(\theta)p(y|\theta),$$

where $p(\theta|y)$ is the posterior density of the parameters θ given data y, $p(\theta)$ is the prior density of the parameters θ, and $p(y|\theta)$ is the likelihood of the data y given parameters θ (Gelman et al., 2004). The likelihood represents the fit of the model to the data for the fish stock of interest (Punt and Hilborn, 1997). The prior density represents information inferred from other stocks or species (Punt and Hilborn, 1997), and is analogous to specifying parameter bounds or applying penalty terms to the likelihood function in maximum penalized likelihood estimation.

There are generally two types of priors: non-informative and informative. Non-informative priors provide relatively little information compared to the observed data. Informative priors are constructed from other sources of data (e.g., data from other stocks) and can strongly influence model results. Punt et al. (1994) were able to build an informative lognormal prior for the catchability parameter of an acoustic survey. As is more commonly the case, catchability is assigned a noninformative prior because it is not a quantity that can be directly measured. Punt and Hilborn (1997) recommend setting a noninformative uniform prior from 0 to ∞ for log-scale catchability, although this would be an improper prior (i.e., the prior density will not sum to one). For state space methods of estimating time-varying catchability, priors or penalty terms must be assigned to the annual process error deviations in catchability (ε_t in Eqs. 3.10 and 3.11). Generally, these process error deviations are assumed to be normally (Schnute, 1994; Butterworth et al., 2003) or lognormally (Wilberg and Bence, 2006) distributed in white noise and random walk methods.

Regardless of whether full Bayesian or maximum penalized likelihood methods are used, one critical issue that remains unresolved for state space approaches is how to determine the variance for the process error deviations. Observation error of CPUE should generally be estimable from the study design and data, but there is no information in the CPUE data on the variance of the process error (Maunder, 2001; Linton and Bence, 2008). In Bayesian state-space models, observation and process error variances can be estimated as parameters by placing priors on them (e.g., Millar and Meyer, 2000). The variance of the process error deviations is usually difficult to estimate without substantial prior information (Linton and Bence, 2008). Typically, in state-space stock assessment models it is necessary to at least specify the ratio of the variances of observation to process error (Schnute and Richards, 1995). An alternative is to specify the variance of process error and allow the model to estimate the variance of observation error, which is also commonly done. However, these methods can lead to overly precise model estimates because they assume that the process error variance or the ratio of the variances is known (Maunder, 2001). Based on a simulation study of variance estimation methods in SCA models, Linton and Bence (2008) recommend using a Bayesian approach to estimate the process and observation error variances. Lewy and Nielsen (2003) attempted to model catchability as a random walk in a Bayesian SCA model, but they determined the model was over-specified (i.e., they were unable to obtain stable estimates of the process error variance for catchability).

Information from other species within a multispecies complex may be useful for estimating a catchability trend for a species of interest. Given the similarities in environmental and biological effects, technological changes, and management changes that simultaneously affect many species in a shared area, changes in catchability may be similar for multiple species within a complex. Approaching estimation of changes in catchability over time as a shared phenomenon may improve the precision of single-species assessments by allowing estimates of catchability to include information on stocks that should have similar patterns of catchability. Although there are other factors that are not shared among species within a complex, dominant factors may be accounted for by using information from related fisheries. For example, relative price may account for changes in relative effort and fisher targeting, while density dependence could control for range expansions and contractions as well as changes in distribution. This method could probably best be used as a prior on the trend in catchability instead of an estimate of the absolute value of catchability.

Expert opinion is sometimes the only source of information available for specifying priors on time-varying catchability parameters. Merritt and Quinn (2000) demonstrate how the perceptions of fishery managers can be used to weight different data sources in an assessment model. Setting these weights is essentially the same as specifying the process and observation error variances associated with each data source. The ParFish approach provides a methodology for using information obtained from interviews of fishermen to set priors on model parameters in Bayesian-based stock assessments (Walmsley et al., 2005). Priors based on expert opinion are more easily evaluated and defended when constructed using a formal methodology, such as those described above.

Combinations of Methods

Any of the above methods can be combined using a state space approach. For example, step functions could be combined with random walks to allow for large known changes in catchability at specific times and gradual changes at other times. Additionally, the parameters of a density-dependent catchability relationship could be allowed to vary over time (Fournier, 1983). Ianelli and Fournier (1998) used a combination of a random walk and white noise model for catchability in an SCA (NRC, 1998). Although the implementation of state-space models described above does not include causal mechanisms for change over time, causal mechanisms can be included in state space models (e.g., Fournier, 1983; Methot, 2000). However, combinations of methods produce more complicated models, and the data may not be informative enough to estimate all of the parameters without auxiliary information or informative priors.

A combination of methods can be used for different indices of abundance within the same assessment. Wilberg et al. (2005) used a Bayesian state-space framework to allow fishery catchability to change over time using random walks, but assumed constant catchability for fishery-independent surveys. This approach can allow the analyst to tailor the assessment model to the specific characteristics of data availability for a given stock.

COMPARISONS OF METHODS

Results can differ substantially among models that make different assumptions about time-varying catchability (Pope and Shepherd, 1985; Wilberg and Bence, 2006). Nearly all methods outlined have been applied in the three types of assessment models included in this review. However, there has been little formal evaluation of alternative methods for incorporating time-varying catchability in assessment models (NRC, 1998). This lack of evaluation of alternative models has also extended to the amount of information necessary to estimate parameters of a time-varying catchability model. For some data sets, catchability and abundance will be too confounded to estimate both. For models that only include a single index of abundance, such as many surplus production models, this is likely to happen with one way trip data, where the index of abundance and catch show a monotonous increase or decrease. For age-structured models it is less clear when estimation will fail. Conflicts in trends among abundance indices can also cause assessment models to fail to produce reliable estimates.

A related problem is that while overall time-varying catchability is estimable in many assessments, its components, such as availability and retention, are not estimable without auxiliary information. Additionally, changes in age- or length-based patterns in catchability (i.e., selectivity) may also be confounded with changes in overall catchability, which can pose problems for models that include a separability assumption (i.e., fishing mortality for a given age or length is the product of overall catchability and an age- or length-specific selectivity pattern (Quinn and Deriso, 1999)). Thus, it can be difficult to determine why catchability is changing over time.

Several studies have compared performance of different methods for fitting (or tuning) VPAs when catchability varies over time. Pope and Shepherd (1985) found that VPA methods that assume constant catchability work well if catchability does not change over time, but can provide severely biased estimates if catchability changes systematically over time. Patterson and Kirkwood (1995) also found that the ADAPT and Laurec-Shepherd VPA methodologies that assumed constant catchability produced biased estimates of spawning stock biomass and total allowable catch when catchability increased over time, but the ADAPT method produced less biased estimates. Pope and Shepherd (1985) suggest that methods that allow for systematic changes in catchability are most robust to trends in catchability over time than methods that do not. However, they warn that estimating time-varying catchability could lead to estimation problems. Marchal et al. (2003) applied extended survivors analysis (XSA) models with and without an estimated linear increase in catchability over time to data from four stocks in the North Sea. They found that assessment models that allowed increasing catchability had less residual pattern, smaller standard errors, and less retrospective pattern than models with constant catchability for three of the stocks.

Wilberg and Bence (2006) evaluated four methods for allowing catchability to vary over time in SCAs: ignoring fishery-dependent CPUE, density-dependent catchability, white noise, and random walk. All of the estimation methods, except for density dependent catchability, were able to estimate time-varying catchability and abundance in more than 99% of the simulations attempted. For the density-dependent model, the parameters of the density-dependent relationship were confounded when density dependence was not present. They found that the best method to incorporate time-varying catchability depends on how catchability varies over time and the amount of observation error in the CPUE time series. Including fishery-dependent CPUE data in the estimation model and allowing catchability to follow a random walk provided the best (or nearly best) estimates of biomass in the last year in most cases (Wilberg and Bence, 2006). The estimation model that ignored fishery-dependent CPUE data performed well when good (coefficient of variation = 25%) fishery-independent survey data were available, but performance degraded as survey precision decreased. The white noise estimation model performed well when catchability did not trend over time, but produced substantially biased estimates when catchability trended over time. The density-dependent catchability estimator performed poorly when catchability was not actually density dependent. They recommended that the random walk method should be used as a starting point for SCAs. Likewise, Labelle (2005) found that modeling catchability as a random walk performed well under a variety of conditions including an increasing trend in catchability in a simulation study of the MULTIFAN-CL model (Fournier et al., 1998).

CHOOSING AMONG METHODS

The best method to model time-varying catchability may be estimated using model selection methods (e.g., Burnham and Anderson, 2002; Spiegelhalter et al., 2002). If models only differ in their fixed effects, then Akaike's Information Criterion (AIC) can be easily applied to determine evidence in favor of one model over another (Akaike, 1973; Burnham and Anderson, 2002). This could be useful for comparing among models with a constant catchability, time blocks of different lengths, polynomials of time, density-dependent catchability, or functions of environmental variables. Additionally, likelihood ratio tests could be used for some comparisons (e.g., Fournier, 1983; Prager, 1994), but the standard methodology only applies to nested models.

A potential detraction of using state space methods to incorporate time-varying catchability is that most standard model selection methods, such as likelihood ratio tests or AIC, are not easy to implement in nonlinear models that differ in their random effects (Burnham and Anderson, 2002). Because of these complications, Wilberg and Bence (2008) explored using deviance information criterion (DIC; Spiegelhalter et al., 2002) to select the best model when state space models were included in the model set. They found that DIC was generally able to select the assessment model that was most similar to the data-generating model, but this did not lead to a general improvement in the accuracy of estimates of biomass or fishing mortality in the last year of the assessment. Bayes factors (e.g., McAllister and Kirchner, 2002) or Bayesian model averaging (e.g., Patterson, 1999; Hammond and O'Brien, 2001) may also be useful options for comparing models when they differ in their random effects.

Often, studies of model selection rely on very similar models for data generation and estimation. This may lead to non-robust conclusions about how well these methods will perform in the real world (Prager, 2002). For example, Prager (2002) found that the presence of outliers caused likelihood ratio tests to select a more complicated surplus production model even though the data were generated from a simpler logistic production model. However, simulation studies are the only feasible way to conduct wide-scale testing of these methods. Evaluations of model selection methods should include a wide range of data generating scenarios, and effectiveness of model selection methods should be compared on multiple scales, such as ability to choose the "correct" structural model and ability to choose the model that makes the most accurate predictions.

SUMMARY AND RECOMMENDATIONS

Time-varying catchability is a common feature of many fisheries. More importantly, trends in catchability also seem to be common, which can lead to biased results from stock assessment models and biased management advice (Pope and Shepherd, 1985; Patterson and Kirkwood, 1995; Wilberg and Bence, 2006). To account as well as is possible for the many known causes of time-varying catchability, CPUE should be standardized for known factors that affect catchability, while recognizing that it will be difficult to correct for all potential causes. Therefore, assessment methods that incorporate time-varying catchability should be used when conducting stock assessments even if CPUE has been standardized unless compelling reasons to assume constant catchability are advanced. Descriptive methods, such as random walks, may produce more accurate estimates than methods that use functional relationships of catchability with other variables if major factors affecting catchability are excluded (Wilberg and Bence, 2006). However, methods that imply commonly occurring functional relationships, such as density-dependent catchability, have many studies from which to derive priors or constraints on parameters and may provide parsimonious descriptions of catchability changes over time. Therefore, multiple methods that apply a range of assumptions about time-varying catchability should be attempted. If time only permits one method and sufficient data are available, random walks appear to perform well under a wide variety of conditions (Wilberg and Bence, 2006). If data are lacking such that these methods cannot be applied, and density-dependent catchability is suspected, functional relationships between density and catchability could be used.

Fishery-Independent Indices of Abundance

Fishery-independent indices of abundance are often among the most important components of a stock assessment. Surveys that use a standardized design and cover the full potential range of the stock will be least prone to time-varying catchability. Under these conditions, constant catchability should be assumed. However, some studies have suggested that even these types of surveys may still be affected by density-dependent catchability, which may be caused by density-dependent changes in fish behavior (Godø et al., 1999) or gear saturation (Rodgers et al., 2003). In addition, if systemic changes in environmental conditions occur as is expected in many regions under climate change scenarios, time-varying catchability in research surveys may become more common. Thus, sensitivity analyses that allow catchability to vary over time may be useful to test for evidence of time-varying catchability.

Changes in survey methods or vessels over time are fairly common features of many research programs. If survey methods have changed and standardization has not been conducted, catchability should be estimated separately for each period, which can be accomplished using a step function. Standardization studies can be used to correct for changes in catchability prior to inclusion in an assessment or to develop a prior on the amount of change from one period to the next.

Surveys that do not cover the whole range of the stock are common. However, including such surveys in a stock assessment can be problematic because they may only be an index of local density rather than abundance of the whole stock. Methods to allow catchability to vary over time can be used to include these data in stock assessments in a fashion that recognizes their limitations.

Fishery-Dependent Indices of Abundance

Fishery-dependent indices of abundance are commonly used in stock assessments and are often the only available source of information on relative changes in population size. Yet, fishery-dependent indices of abundance are more likely to be affected by time-varying catchability than fishery-independent indices because fisheries often target specific stocks and change gears and methods over time. Some have suggested that fishery-dependent indices of abundance should not be used if fishery-independent indices are available (NRC, 1998). Wilberg and Bence (2006) found that ignoring fishery-dependent indices of abundance only worked well when the fishery-independent index of abundance was fairly precise. Including fishery-dependent indices of abundance in an assessment that allows catchability to vary over time can produce more accurate abundance estimates than simply ignoring fishery-dependent indices. To account as well as is possible for the many known causes of time-varying catchability in fishery-dependent indices, CPUE should be standardized, and methods that allow time-varying catchability can be used to include these data in stock assessments in a manner that recognizes their inherent limitations, as in the case of surveys that do not cover the whole range of the stock.

Additional Data Collection

Collecting additional data may help in determining whether time-varying catchability is occurring for a given stock. To assist in CPUE standardization, collection of data that allows better characterization of fishing effort, such as fishing location and fishing technology used, should allow improved standardization of fishery CPUE. For some fisheries with vessel monitoring systems this should be relatively easy to obtain. For others, such as recreational fisheries, it could be very difficult to obtain because of the number of participants in the fishery and their often wide spatial and temporal distribution. Martell and Walters (2002) suggested that directly estimating exploitation rate and catchability could be done with fairly modest mark-recapture studies in some fisheries. Mark-recapture data can also be integrated with other kinds of assessments fairly easily (e.g., Coggins et al., 2006), which could provide additional information to detect changes in catchability. Data on other aspects of fish population and fisheries, such as range of the stock and spatial distribution of fishing, may be useful to determine stock status and whether catchability has changed, and Walters and Martell (2004) have recommended that these be routinely evaluated.

Use in Management Strategy Evaluation (MSE) and Stock Projections

MSEs are becoming widely used to compare and choose procedures for managing a fishery. These studies rely on development of one or several "operating models" that simulate the underlying population dynamics, fishery, data collection, stock assessment, and management (Butterworth, 2007). The development of the operating model often relies on existing stock assessments to inform parameter values and processes for inclusion (Butterworth, 2007). The methods outlined in this article can provide base models that can be used in MSE. However, the descriptive methods, particularly the random walk and polynomial methods, may cause problems for simulating data sets because they can potentially drift to positive or negative infinity. Thus, assessment models that use functional relationships may be useful for parameterizing MSE operating models. First order autoregressive processes could potentially be used instead of a random walk model to represent similar dynamics while maintaining a stationary mean.

Stock projections are often conducted to evaluate fishery responses to alternative management proposals (Hilborn and Walters, 1992). Similar to the construction of operating models for MSE, stock projection requires alternative assumptions regarding future changes in catchability when policies that consider effort management or use of CPUE in harvest determination are evaluated. The projection of future changes in catchability can be accomplished using the first order autoregressive processes or functional forms for catchability, and prior studies may be used to formulate likely hypotheses. For short-term projections, it may be reasonable to assume catchability is constant at the value of the last year or an average over the last several years.

Research Recommendations

More studies are needed to compare the performance of the different methods for including time-varying catchability in assessment models and to test methods for selecting among models. A particularly important component is understanding when time-varying catchability is estimable in situations where data are limited because highly parameterized state-space models may not perform well under these conditions. Research on performance of time-varying catchability methods is needed for simpler stock assessment models because most studies on performance have only used age-structured models. Few studies have attempted to develop or evaluate methods to objectively decide among competing stock assessment models. Given the number of potential methods that could be applied, development of reliable techniques for deciding among multiple techniques is needed.

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