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Catchability: a key parameter for fish stock assessment

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Catchability rationale

The fishing process in a particular fishing ground involves the existence of one or more fish populations in different stages of their life cycles, with a particular behaviour according to natural or foreign challenges; their abundance depends on biological and environmental conditions and they must be captured by fishermen with sophisticated equipment known as fishing gears. This capture is known as fishing mortality and depends on the resource abundance and the efficiency of the fishing gear. The relationship between these two variables is known as catchability. In other words it measures the interaction between the resource and the predation effort.

If the catch or fishing mortality is taken as an indication of population size, it is necessary to learn how representative is this catch of the whole population. The implications of such an assumption have been incorporated in the following relationship:

$$C = sqEN \text{ or } U = C/E = sqN \quad (1)$$

where C denotes catch, which is equal to F (the fishing mortality), U is catch per unit effort, E is the fishing intensity or fishing effort, s is a constant related to the particular fishing gear, q is the catchability coefficient, and N is the population size. The importance of the catchability coefficient cannot be overestimated.

Catchability has been defined as a measure of the interaction between the resource abundance and the fishing effort. Baranov (1918), Gulland (1964, 1983) and Caddy (1979) defined the catchability coefficient as the proportion of individuals in a fishing

ground of size A removed by a gear sweeping an area a with efficiency c , i.e. $q = c(a/A)$. Although this approach considers the physical characteristics of the gear, it leaves aside the fish behaviour and fishing strategy which also affect the catch. So, catchability may be better defined as the fishing mortality per unit of effort or unit of fishing intensity, $q = F/E$, which can be interpreted as (a) the number of fishes or biomass per unit of fishing effort, so reflecting variations in abundance (Beverton and Holt, 1957); or (b) if the population or abundance is constant or in steady state and the fishing effort is also constant, variations in q will reflect fish vulnerability to fishing gear, fishing strategy, and fish biology, including behaviour and response of individuals to environmental factors.

Recent developments in fisheries ecology (MacCall, 1990; Christensen and Pauly, 1992) give an alternative interpretation to this definition. A is considered the area of the whole population habitat, a the fraction affected by the fishing gear and c the efficiency of the fishing gear in relation to a given population density. With this new definition, catchability changes may be explained in terms of spatial and temporal fluctuations of population abundance, interdependencies with other species and fishing effort.

Catchability research has developed either to give a measure of the fishing gear efficiency, or to find the relation between population size and fishing effort. Whatever the adopted approach, the interpretation may be elusive unless there is a clear understanding of other associated concepts, such as selection, selectivity, accessibility, availability and vulnerability. All of them are sources of catchability variation and under special situations may be equally interpreted (Sakuramoto and Tanaka, 1986).

Selection (s) is the probability of retention of fishes of a given size by a fishing gear, providing a measure of the degree of escapement. If this concept is applied to the relationship $q = c(a/A)$, it is clear that selection will reflect on the specific efficiency (c) of the fishing gear; in this case catchability and selectivity are similar for those fishes with a retention probability (s) equal to 1. Ralston (1990) defines this situation as 'full selection' catchability.

The concept of catchability as the relation between abundance and fishing effort needs some elaboration. Fishery biologists often assume that a fish population is evenly distributed in a given area and that fleets have complete access to it. This may be the case if appropriate fishing strategy and gear are adopted. It is especially true for knife-edge recruitment, though in many cases may be questionable, i.e. small-scale, artisanal or some continental shelf fisheries. If these conditions are not met, there are biases on population size and fishing mortality as the fishery will be acting on a portion of the population, and measurements of catchability and fishing mortality will be made on the fraction of the population exploited. This is particularly important for the dynamics of short-lived species like some clupeoids, squids and shrimps, as well as for seasonalities in population processes (i.e. migration, recruitment). Both assumptions, accessibility and availability, are related to spatial distribution of the fishing effort and of the fish resource, affecting the area ratio a/A . If this ratio remains constant, catchability will depend on the efficiency c .

Vulnerability is related to the probability of encounter of the fishing gear and fish; if fish is available, vulnerability will depend on fishing gear efficiency apart from the selection probability s . If this value is 1, efficiency will rely on fishing strategy.

The concepts discussed above implicitly assume identical behaviour of all fishes in

the population including their interaction with the fishing gear. Under this ideal behaviour, the relationship $q = c(a/A)$ will vary among individuals, while catchability patterns will reflect fish and fishery behaviour.

Catchability as a measure of fishing success depends in part on the gear efficiency. A great deal of effort has been expended in improving the catching capacity of gears considering fish behaviour and fishing techniques among others. Penn (1984) describes how catchability is affected by shrimp behaviour to different trawl design and operation, levels of aggregation and schooling patterns. Chittellborough (1970) and Morgan (1974) studied the effect of water temperature on catchability, on the assumption that the activity of the fish increases with the increase of water temperature, therefore increasing catchability. They found that the catchability value doubled with temperature changes from 18 °C to 24 °C and tripled from 16 °C to 22 °C, while Morrissy and Caputi (1981) found that over a temperature range of 14 °C to 22 °C, the catchability of large and small crayfish, *Cherax tenuimanus*, increased by a factor of two and five respectively. Hill (1985) related temperature to duration of emergence, speed of return to shelter and catchability of the tiger prawn *Penaeus esculentus*.

Wassenberg and Hill (1990) describe moulting behaviour of *P. esculentus*, suggesting that the corresponding inactivity periods affect vulnerability, and Miller (1990) discusses how it affects catchability. Ivanov and Stolyarenko (1988) discussed how tidal cycles modify the orientation of shrimps and trawl, affecting catchability. Both studies show how variations in shrimp activity can be used to increase trawl efficiency.

Ehrich and Groger (1989) analysed the diurnal variation in catchability of several fish species in the North Sea. The sources of variation were (a) time of day, (b) wind strength and (c) wind direction relative to the course of the vessels. Time of day strongly influenced the catch of cod (*Gadus morhua*, Gadidae), haddock (*Melanogrammus aeglefinus*, Gadidae) and herring (*Clupea harengus*, Clupeidae), being in all cases significantly greater during daylight. The only exception was whiting (*Micromesistius pontassou*, Gadidae), which was not affected.

Ko and Kim (1984) investigated changes in catchability with different trap designs; Yamane and Itaka (1987), Yamane and Flores (1989) and Yamane and Fujishi (1992) evaluated the efficiency of small pots for prawns on the basis of entrance and escape behaviour. Collins (1987) increased catchability by changing 36-mesh monofilament nets to deeper 50-mesh nets in the commercial fishery in Lake Huron. Moriyasu *et al.* (1989) tested traps with different catch characteristics for snow crab, *Chionectes opilio*; and Miller (1990) discussed different factors affecting selectivity of crab and lobster traps.

Dorel *et al.* (1985) related catchability changes in sole (*Solea vulgaris*, Soleidae) nurseries to fishing gear efficiency (selectivity and scraping); fish behaviour (avoidance, escaping, burying), and environmental conditions (currents, depth, illumination, turbidity). They found that the main factors affecting catchability are scraping and burying (by the addition of a tickler chain in front of the ground rope increasing apparent abundance threefold), and the tide, with greater abundance during ebb.

The examples given above show the relation between catchability and fish gear and fishing strategy.

Managing techniques aim at regulation of fishing mortality either among the adult population or at specific stages of development. Resource abundance and fishing mortality constitute the basic estimates of fish stock assessment; catchability is involved in both evaluations.

Control of fishing mortality may be implemented in various ways: some, like catch quotas or closed seasons, do not require specific estimation of catchability because the control is on the amounts of fish caught, or surviving in the absence of fishing; however, catchability provides useful information on trends in abundance from survey data. If control is carried out through fishing effort, then catchability becomes an essential parameter, because of its relationship to yield and abundance.

Most of the existing population dynamics literature does not deal with catchability *per se* but with its application to yield models, where it is usually taken as a constant parameter; this assumption affects the quality of those models. This subject is widely discussed in the existing literature, being a source of frustration to fishery biologists. Catchability is not constant but highly variable, and the sources of variation and relative importance depend on the exploited population. This is well illustrated with the clupeoid fishery because of its serious implications; here vulnerability increases as abundance decreases (MacCall, 1976, 1990; Murphy, 1977; Csirke, 1989). Ricker (1975: 155) stated that catchability variability is likely to be the greatest source of error in models based on catch per unit of effort with catchability constant.

Of particular interest in managing techniques is the incorporation of fish aggregation devices (FADs) and artificial habitats which promote fish aggregation in small areas, reducing the fishing effort and increasing fishing efficiency. The risk is that aggregation increases catchability and the reduction of fishing effort may promote undesirable higher mortality, i.e. affecting survival or recruitment. The relation of catchability with FADs will be discussed in greater detail below.

Evaluation of the catchability coefficient

One of the first models to incorporate a catchability parameter was the estimation of population size in closed system (Leslie and Davies, 1939). Here catch per unit effort (U) was assumed to be an index of population density. The mathematical expression is:

$$U(t) = q[N_0 - C_c(t)] \quad \text{or} \quad q = U(t)/[N_0 - C_c(t)] \quad (2)$$

where $U(t)$ is the catch per unit of effort at time t , q is the catchability coefficient, N_0 is population size in numbers at beginning, $C_c(t)$ is cumulative catch at time t . So catchability q is interpreted as the proportion of population abundance at time t with respect to the remaining population after a fraction of the initial population has been removed (C_c); here catchability depends on population density.

A similar equation suggested by DeLury (1947) expresses changes in population abundance as a function of the accumulated fishing effort:

$$U(t) = qN_0[N(t)/N_0] \quad (3)$$

where $N(t)$ is population size at time t , and other symbols have the same meaning as above. Because the fraction of the stock taken by a unit of fishing effort is small, the quotient on the right side can be used to express the fraction of the stock remaining after application of the fishing effort, so the model is described by

$$U(t) = qN_0[e^{-qE_c t}] \quad (4)$$

where E_c means the cumulative fishing effort. In this model catchability is interpreted as in the Leslie and Davies equation.

The Silliman (1943) and Paloheimo (1958) models are as follows

$$Z(t) = M + qE(t) \quad (5)$$

with Z being the instantaneous rate of total mortality, M the instantaneous rate of natural losses (assumed as constant), and E the fishing effort. Here, catchability is given by

$$q = [Z(t) - M]/E(t) \quad (6)$$

Because Z and M are related to changes in number of fishes per unit of time, catchability is directly interpreted as the change in numbers of fishes per unit of time and unit of fishing effort. In this case, it is a direct measurement of the fishing mortality caused by one unit of fishing effort.

Tagging techniques may assist in evaluating catchability, as they provide direct measurements of population density (extensive review: Pollock *et al.*, 1990). This information, combined with fishery data (catch and effort) can be related as:

$$q = cpue/D_p \quad (7)$$

where $cpue$ means catch per unit of fishing effort (CPUE) and D_p denotes population density. In terms of the number of fish tagged (Chapman, 1965):

$$q = \sum_{i=1}^k m_i l \sum_{i=1}^k E_i \bar{T}_i \quad (8)$$

where m is tag recaptures, E is fishing effort, T is the tagged population and i is a period of time;

$$T_i = (T_{i-1} e^{-M\Delta i} - m_i)$$

and

$$\bar{T}_i = \{T_{i-1}(1 + e^{-M\Delta i}) - m_i\} l 2,$$

expressing the average abundance of tagged fishes.

All the above representations of catchability are different forms of the basic equation

$$C = sqEN \quad \text{or} \quad q = \left(\frac{1}{s}\right) \left(\frac{1}{N}\right) \left(\frac{C}{E}\right) \quad (9)$$

In this regard, catchability may be taken as:

- catch per unit of fishing effort (numbers)/remaining population (assuming a closed system, as represented by Equations 1, 2 and 3);
- number of fish caught (C) per unit of fishing effort ($E = 1$)/number of fish present in a given area (if N represents population density) (Equations 7, 8 and 9);
- fishing mortality/fishing effort, where fishing mortality is the number of fish killed (C)/numbers in population (Equation 5).

As indicated above, catchability may be interpreted in various ways according to the model; some express population in units of biomass while others consider the fish as the elementary population unit. However, none of them take into account population structure regardless of the fact that when population is expressed in biomass or elementary fish units, catchability is implicitly assumed to be constant among

individuals over time, fishing effort is taken as uniformly distributed and of constant quality, and population size is considered constant. Therefore the meaning and interpretation of catchability will also be different depending upon how population units are chosen.

A different interpretation of catchability is given when dealing with population structure such as the dynamic pool model (Beverton and Holt, 1957) and/or an age/size structured model such as the age/length VPA (Gulland, 1965; Murphy, 1965; Pope, 1972; Jones, 1974, 1981). In the last case, mortality, particularly fishing mortality $F = qE$, is assumed to be changing with age. As a result, most of the expected changes with age will result from variations in catchability q , except when fishing effort E is targeted at specific ages, as a form of selection. The catchability parameter must be evaluated for each age or size class because the fish behaves differently according to its stage of development, area of distribution and particular attitude when in contact with the fishing gear. All these aspects, together with time variations, affect catchability.

Although fishing mortality is estimated similarly in structured models, age-VPA and length-VPA may give different results and interpretations of catchability. In the first case, each age class is identified as a specific cohort, meaning that all fishes belong to the same generation or are coming from the same reproductive cycle. In such a case, catchability incorporates cohort-inherent characteristics, i.e. cohort strength, which are not shared by other cohorts, such as reproduction taking place when environmental conditions are adequate for early-stage development, implying healthier fishes for survival and development. This process affects relative fish vulnerability to capture.

In the case of length-VPA, it is assumed that catchability varies with size, which is not typical of cohort behaviour. Catchability preferences between cohorts may be identified. They are likely to be mixed with interannual changes or reflect fish reaction to fishing gear. Typical examples are fish aggregations, where size is directly related to selection.

One constraint of the age/length-VPA using fishing effort data is the need to assume a catchability pattern. In general this assumed pattern follows an exponential function (Pope and Shepherd, 1985; Megrey, 1989). However, this assumption may not hold for some species, as would be the case when vulnerability of a developmental stage is higher than that of others, for example spawners during aggregation. Here, again, catchability evaluation is crucial. Another problem with VPA is that errors involved in the catchability assumption are accumulated during the VPA back-calculation, introducing errors in fish mortality evaluation. Megrey (1989) discussed some limitations when some age-structured models are applied and two common assumptions concerning catchability are taken: (a) it does not vary by age and year, and (b) it is independent of the stock size (Table 1). His main conclusions pointed out the sensitivity of the models to trends in catchability and some problems related to estimating year classes. Regarding catchability estimates, some of the analysed models can estimate catchability, but practically none do this by age or year, or consider density-dependent catchability.

In multigear fisheries there is a catchability coefficient for each gear because of the vulnerability of the fish to the particular fishing gear, while the efficiency of the gear will be related to population characteristics. Another case will be the evaluation of the catchability coefficient under various fishing efforts, but with similar gears. Special care has to be taken in the interpretation and use of catchability coefficients evaluated

Table 1. Limitations related to catchability in age-structured models (adapted from Megrey, 1989). VPA, Gulland (1965) and Murphy (1965); DOUB, Doubleday (1976); P&S, Pope and Shepherd (1982); PALO, Paloheimo (1980); F&A, Fournier and Archibald (1982); DUP, Dupont (1983); DER, Deriso *et al.* (unpublished, in Megrey, 1989: 36)

	VPA	DOUB	P&S	PALO	F&A	DUP	DER
<i>Assumptions</i>							
Catchability of the gear is constant and does not vary by age and year	Na*	Na	Na	Yes	Opt	Yes	Yes
Relationship between fishing effort and fishing mortality is independent of the stock size	Na	Na	Na	Yes	Opt	Yes	Yes
<i>Advantages</i>							
Estimates of F can be used to test more effectively the proportionality of F to effort (i.e. $F = qE$) and the validity of CPUE	Yes	Yes	Yes	No	Yes	Yes	Yes
<i>Disadvantages</i>							
Model is sensitive to trends in catchability with effort or time	No	No	Yes	No	Yes	No	Opt
If data from just one cohort are being analysed, the linear model will not do well at estimating the year class abundance parameter because it is highly correlated with catchability	No	No	Yes	No	No	No	No
<i>Estimated parameters</i>							
Catchability	No	No	No	Yes	Yes	Opt	Opt
Catchability by age	No	No	No	Opt	No	No	No
Catchability by year	No	No	No	No	Opt	No	No
Density-dependent catchability	No	No	No	No	Opt	No	No
<i>Parameters required</i>							
Catchability estimates for other ages	No	No	No	Yes	No	No	No

*Na, not applicable; opt, optional.

from fishing effort data reported in different units; for instance, in a trawl fishery, reporting vulnerability of fish per unit area and unit time is very different from reporting vulnerability of individuals per fishing trip.

Another matter that affects both catch per unit of fishing effort (U) as a measure of

abundance, and catchability (q), is the fishing effort, when individual fishing power is significantly different between boats and/or fleets. Most of the time, nominal fishing effort is used in assessment work; however, accurate catchability estimations require a more careful analysis, with appropriate standardized units of fishing effort or effective fishing effort.

Catchability coefficients have been used for other purposes of population dynamics. Moffit and Polovina (1987) evaluated the unexploited biomass of three species of deep-water shrimp (*Heterocarpus* spp.) in the Mariana Archipelago, based on catchability, relative abundance and habitat area. Ugland (1985) estimated the population size of the harp seal considering that each age group has its own catchability and vulnerability when hunting.

It is stressed that catchability coefficients are valid only for the conditions under which they were taken. Application of a constant coefficient implies that:

- estimations apply to individuals with similar catchability;
- estimations apply to the conditions under which the data were obtained (e.g. temperature, area);
- fishing effort is of the same quality;
- the population is closed.

It has been mentioned that the catchability coefficient can evaluate the effect of fish aggregation devices (FADs), which concentrate fish in a small area to facilitate catch. Its rationale is as follows: a population (N) is present in a certain area (A); a fishing gear operating here has an area of influence (a) and interacts with a part (n) of the population. According to its technological characteristics, the fishing gear will retain fishes of certain sizes (selection, s) and taking the fishing gear as the unit of effort E , catchability (q) can be defined as:

$$q = \{s[(n/a)/(N/A)]/E\} \quad (10)$$

where (n/a) represents the fish density in the area of influence of the fishing gear and (N/A) the population density in the total area A .

FADs are so named because they produce accumulation of fishes (n') in the area of influence of the fishing gear by decreasing abundance in other areas (N'). So assuming that s and E remain constant, catchability under FADs will be:

$$q' = \{s[(n'/a)/(N'/A)]/E\} \quad (11)$$

where $q' > q$ because $(n'/a) > (n/a)$ and $(N'/A) < (N/A)$.

Polovina and Sakai (1989) explain increments in the population size of the octopus, *Octopus dolfeini*, from Hokkaido Bay, Japan as generated by FADs. Arreguín-Sánchez and González-Cano (1996) suggest a similar behaviour for the lobster fishery of Cuba, where the fishing strategy makes a more efficient use of the energy available in the ecosystem which is not fully used by the thermodynamics of the ecosystem. The mechanism responsible for it is that there is an excess of larvae which are prevented from settling by density dependence effects. Because of the operation of FADs, adults are concentrated at specific areas (containers) and a 'vacuum' in the habitat is produced; this becomes occupied by part of the surplus, producing a net increment in population size.

Catchability patterns

The first studies involving catchability patterns were developed for clupeoid fisheries. Under the current perspective of scientific knowledge this is not strange because the contraction–expansion behaviour of fish schools results in increments in catch with decrements in population abundance.

Gulland (1964) for the purse seine fisheries and Ostvedt (1964) for the Norwegian winter herring expressed doubts on the validity of catch per unit effort to evaluate population abundance. The first reports on the inverse relationship between catchability (fishing success) and population abundance for clupeoid fishes were those of Paloheimo and Dickie (1964), Murphy (1966), Schaff and Huntsman (1972), Radovich (1973), Pope and Garrod (1975), MacCall (1976) and Ultang (1976).

Another problem is the way in which we can obtain the patterns of catchability changes with respect to any of the variables (sources of variation) mentioned for the models above. For example, there is little direct evidence on how catchability changes with age or size, especially from information taken from commercial vessels. The only feasible way to obtain this information is through mark–recapture experiments like that developed by Ehrdhardt (1990) from sequential tagging experiments and fishery data. This author used the maximum likelihood equation given by Chapman (1965) for the stone crab (*Menippe mercenaria*) in Everglades National Park.

Attempts to estimate catchability patterns from age/size are usually based on indirect estimation when age/length-VPA is applied. When long time series of data are available, and cohort analysis is carried out for a number of years, acceptable general catchability patterns can be obtained. This type of approach was applied by Csirke (1989) for the Peruvian anchoveta (*Engraulis ringens*, Engraulidae) and by Arrizaga and Veloso (1982) for the common sardine *Clupea (Strangomera) bentincki* from Talcahuano, Chile.

When long time series of data are not available, an assumed catchability pattern with age/length is usually based on the experience of the fishery biologist. A number of these applications are described by Pope and Shepherd (1985). Table 2 summarizes various studies related to the inverse relationship between catchability and abundance.

Some work has been done on structured models considering the partial contribution of cohort to catchability. Megrey (1989) reviewed age-structured stock assessment models, identifying the limitations imposed by assumptions about catchability (Table 1).

Age-structured methods take into consideration age-dependent catchability, and in some cases interannual changes (as a form of time dependence catchability), or age-time dependent catchability in cohort analysis; however, seasonal variations of abundance or density dependence are not included. In fact, these variables are neglected, assumed constant or, in the best case, assumed independent of other sources of variation.

Seasonal variation of abundance in age-VPA models constitutes a serious problem for some fisheries because of the assumption that catches are equally distributed throughout the year. Sims (1982) proposed a form to correct for this in fishing mortality estimation; however, it does not solve the problem because it does not incorporate seasonal variation in abundance.

Apart from seasonal variation there are other environmental conditions that may enhance the production of biomass, as clearly shown by upwelling regions in the world

Table 2. Studies reporting a relation between catchability, q , and population abundance

Author	Catchability model or coefficient	Observations
MacCall (1976)	$q = aU^{-b}$	California purse seine sardine. U = CPUE, a , b , constants.
Utlang (1976)	$U = \alpha N^{\beta+1}$	Atlanto Scandian herring. U = CPUE; N , abundance; α , β , constants.
Peterman and Sterr (1981)	$q = \alpha N^{\beta+1}$	Chinook salmon sport fishing.
Bannerot and Austin (1983)		Yellowtail sport fishing, Florida. N , population abundance; α , β , constants.
Cooke (1985)	$C = qEN^{\rho}$; $\rho < 1$	Whales. C , catch; E , fishing effort; N , population size.
Quinn (1987)	$q_t = q_0 e^{-r_1}$ $r_1 = \alpha_1(t)$; $r_2 = \alpha_2 E(t)$	e , fishing effort.
Angelsen and Olsen (1987)	$q = \alpha E^{-\beta}$	Cod fishery, Lofoten. E , fishing effort; α , β , constants.
Csirke (1988, 1989)	$q = aB^{-b}$	Peruvian anchoveta. B , biomass; a , b , constants.
Arreguín-Sánchez (1989)	$q(a) = \alpha \exp^{\beta_{age}}$	Red grouper fishery, southern Gulf of Mexico. α , β , constants.
Grecco and Overholtz (1990)	$q = 0.085N^{-0.384}$ $q = 0.287Area^{-0.278}$	Haddock, Georges Bank. N , population abundance; $Area$, population habitat.
Rose and Leggett (1991)	$q = 0.095B^{-0.787}$ $q = 0.003Area^{-0.747}$	Cod gillnet fishery, Atlantic. B , biomass; $Area$, population habitat.
Hilborn and Walters (1992)	$q_t = q_1 \left[\frac{T/q_2}{1 + q_3 B_t} \right]$	Peruvian anchoveta. q_1 , base fraction per unit of effort; B , biomass; T , temperature; q_2 , q_3 , constants.

oceans. The Climate and Eastern Ocean System Project (CEOS) (Bakun *et al.*, 1992); the Peruvian anchoveta (Pauly and Tsukayama, 1987; Pauly *et al.*, 1989), and the fisheries of the western coast of Africa (Cury and Roy, 1991) are typical examples.

Sissenwine and Bowman (1978) discuss catchability variations and factors related to bottom trawls; Linfield (1980) studied the artificially stocked population of the common carp (*Cyprinus carpio*, Cyprinidae) in Grey Mist Mere, a South Lancashire lake, in tag-recapture experiments and found that in the case of angling, the first capture did not significantly decrease further capture.

Gordoa and Pereira (1987) found errors in catchability fluctuation due to errors in the estimation of fishing mortality produced by variation in discards, and not considering variation in natural mortality rates by density-dependent factors. In this regard, Stokes and Pope (1987) concluded that realistic trends in catchability may not be detectable from catch-at-age and commercial data, using a multiplicative model to simulate variability of catchability with time. Shardlow and Hilborn (1985) and Peterman *et al.* (1985) discussed the measurement of population abundance and found that conclusions

may be biased if errors in their measurements are not considered, suggesting inappropriate catchability patterns.

Implications of catchability assumptions in fisheries models

Because of the relevance of catchability in the quality of the models it is desirable to analyse the implications of the various assumptions commonly applied in fishery dynamics.

Most yield and population models assume that catchability is independent of biomass abundance. This implies constant fish vulnerability, meaning that the catch per unit of effort is independent of population density. The obvious implication is that under intensive exploitation a switch to overfishing can take place rapidly. If catchability is assumed to vary with biomass abundance, fish vulnerability will also vary in a similar fashion; however, stock behaviour may produce a different result. There are some well-known cases which support this statement, such as clupeoids with schooling behaviour, where catchability increases when abundance decreases. The interpretation is that such a population is composed of several schools dispersed in the fishing ground. As exploitation increases, the size of the schools decreases; the remaining fishes will aggregate in new schools; population and habitat size will decrease and the effectiveness of fishing effort will increase because of decreasing searching effort. This increase in catch is interpreted by fishermen as an increase in abundance, leading to more exploitation; if this situation is prolonged, overfishing may occur.

Another source of violation of assumptions is that abundance is subjected to changes with time (i.e. interannual and seasonal fluctuations), as well as to changes in fish behaviour according to stage of development, both affecting fish vulnerability. Fisherman cope with this problem by changing their fishing strategy. The implications in short-term management are serious.

Even if constancy of catchability is waived, some models require information about the direction or pattern of catchability variation. This is the case for age/length-VPA using fishing effort data. There are two approaches to get fishing mortality from catchability: (a) with catch-at-age/length evaluation of the age/size catchability coefficient, and (b) adopting a catchability pattern from previous age/length data. The first case is truly empirical and the resulting pattern ought to be accommodated to population behaviour. The second one is taken as a response to an expected population behaviour. Usually, estimations are recalibrated with new fishing data.

Making assumptions about catchability patterns requires a good knowledge of fishing operations as well as a comprehensive analysis of some fishery properties in regard to accessibility, the availability of fish as well as their vulnerability. These concepts are not expressed as a parameter in population and yield models, because they are implicitly considered in the catchability value. If no information is available, and assumptions must be made, they will be more appropriate if the implications of concepts above are correctly identified for a particular fishery.

Towards an integrated catchability model

Studies up to the present time show that catchability depends on many variables. When dealing with the performance of fishing gears, fish behaviour is probably the main factor.

Here, life history, ecological relations and interaction with the fishing gear are some aspects to be considered.

Each population in the community and in the ecosystem may react differently to fishing stress. This explains why fishing gears are different, even for the same species in different ecosystems, and why highly diverse communities exhibit also a high variety of fisheries and fishing gears.

Few models incorporate more than one source of variation. The first attempts were those of Grecco and Overholtz (1990) and Rose and Leggett (1991) for the Georges Bank haddock and Atlantic cod respectively, considering both biomass abundance and area (habitat of the exploited stock), and of Quinn (1987) with age and fishing effort. Hilborn and Walters (1992) present a catchability model for the Peruvian anchoveta considering both biomass and temperature (Table 2).

Arreguín-Sánchez (1992) introduced one deterministic model which incorporated various sources of variations based on a long time series of catch-at-length and fishing effort data. The rationale behind it is that catchability as measured by the catchability coefficient is related to the following factors.

1. Size of the fish, as indicated by its length. Length reflects information about growth, survival, the developmental stage and reproduction, as well as selection of fishing gear. Age, in the population, represents information on the history of specific cohorts.
2. The structure of the population, as reflected by its size. Population structure will change with time, so the catchability for different lengths also changes with time.
3. Differences among fishing fleets. Differences in the fish-length catchability pattern imply differences in vulnerability between fleets when they are fishing in the same area with the same fishing gear. The allocation of fishing intensity of a given fleet to a specific range of fish size is associated with fishing strategies, fishing areas, population gradients and fish behaviour; all these give relative differences in vulnerability. These differences could be measured directly from the length composition of the catches.
4. Population density. The term 'density dependence' refers to the influence of intraspecific population density on habitat selection, which is regulated by population size and local density; it affects relative distribution of the population among habitats. However, the sustainability of harvests gives support to the existence of strong compensatory mechanisms in fish.
5. Amount of fishing. This is considered an important source of variation in the size of the exploited populations, and in survival rates, which can vary in each age or length class, being reflected in the population density and the corresponding catchability coefficient. The assumption here is that fishing effort, which is related to the amount of fishing, affects the catchability coefficient through changes of population density.

A fully developed fishing mortality model has to account for: (a) age-specific selectivity of the gear; (b) catchability as a function of age or time; and (c) gear saturation. To accommodate these features, Megrey (1989) suggests:

$$q(a,t) = f\{a,t,s(a), N(a,t,E)^{\varphi} E(t)^{\delta}\} \quad (12)$$

and the generalized fishing mortality model

$$F(a, t) = f\{a, t, s(a), N(a, t, E)^\varphi E(t)^{1+\delta}\} \quad (13)$$

where: s is the selectivity coefficient for age class a ; $N(a, t)$ is the abundance (number) of the age class a at time t ; $E(t)$ is the effective fishing effort at time t or full recruitment fishing mortality; δ is a population density parameter and φ is a gear saturation parameter.

The integrated model proposed by Arreguín-Sánchez (1992) is based on the transition matrix to estimate catchability-at-length from which the relation $q = f(l)$ is obtained:

The transition matrix is described as

$$\tilde{X}(t+1) = A\tilde{X}(t) \quad (14)$$

where: $\tilde{X}(t)$ is the population structure at time t ; A is the transition matrix, which can be expressed as $A = GS$, where G is the growth (probability) matrix and S is the survival matrix. Each element in the main diagonal of S is given by e^{-Zl} with $Z(l, t) = M + q(l, t)E(t)$. Probabilities for G matrix can be assigned following Shepherd (1987).

Because $\tilde{X}(t)$, $\tilde{X}(t+1)$, M and E are known, Equation (14) can be solved assigning values to $q(l)$ to obtain the estimated population structure $\hat{\tilde{X}}(t+1)$. Using a minimum-squares algorithm, differences between observed $\tilde{X}(t+1)$ and computed $\hat{\tilde{X}}(t+1)$ values can be minimized to obtain the best fit for $q(l)$. For long time series, several values of $q(l)$ for each length class l and its corresponding trend can be obtained.

Arreguín-Sánchez (1992) also used the relationship between the yearly ratio of catch per unit effort per length class with length, with respect to the average over a number of years, as an approach to equilibrium.

$$\ln \left[\frac{Uly}{Ul\bullet} \right] = \ln \left[\frac{qlyNy}{ql\bullet N\bullet} \right] \quad (15)$$

where U means catch per unit of fishing effort, l is an index of the length class, \bullet is a symbol for a population under equilibrium and y means time in years. If the population is reasonably stable over time, population abundance $U(y)$ will approach to equilibrium $U(\bullet)$, and

$$\ln \left[\frac{Uly}{Ul\bullet} \right] \cong \ln \left[\frac{qly}{ql\bullet} \right] \quad (16)$$

meaning that the departure of $U(l, y)$ with respect to $U(l, \bullet)$ (abundance at time t , with respect to that at equilibrium, \bullet) will be equal to the departure of catchability at time t with respect to that at equilibrium.

The relationship given by Equation (16) can be expressed as a linear function of the mid-length value of the length class l :

$$\ln \left[\frac{Uly}{Ul\bullet} \right] \cong \ln \left[\frac{qly}{ql\bullet} \right] = \alpha(y) + \beta(y)\bar{l} \quad (17)$$

$$\text{where } \beta(y) = \ln \left[\frac{q(l+1)y}{qly} \right] - \ln \left[\frac{q(l+1)\bullet}{ql\bullet} \right]$$

which is interpreted as the logarithm of the rate of change of $q(l,y)$ with respect to the equilibrium, or in other words, how fast $q(l,y)$ changes with increasing values of fish size at time y .

Each month the same procedure was followed, to obtain monthly departures of catchability-at-length, as represented by the slope $\beta(m)$.

Density dependence was estimated by regressing $\beta(y)$ values against $E(y)$, where the slope, $\beta(E,y)$ is a measure of the density-dependent effect on catchability. This assumes that the key factor affecting fish abundance is the fishing activity.

An analogous procedure is adopted to incorporate several fleets (f), by regressing the ratio of each other fleet against length. For a given year, the slope $\beta(f,y)$ will represent the departure of catchability-at-length of one fleet with respect to the other. This procedure can also be applied for monthly differences between fleets, with a slope $\beta(f,m)$.

All the above sources of variation analysed as departure from the equilibrium or differences between fleets can be incorporated in one single additive model as follows:

$$\beta(l,t,E,f) = \beta(\bullet) + \beta(t) + \beta(E,y) + \beta(f,t) \quad (18)$$

where $\beta(l,t,E,f)$ is the slope of the integrated catchability model $q(l,t,E,f) = f(\text{size})$, which provides catchability estimates without equilibrium constraints and adjusted for the sources of variation considered. The model is also adjusted for selection, using the probabilities of retention (including saturation effect) per length class, previous to the transition matrix estimates.

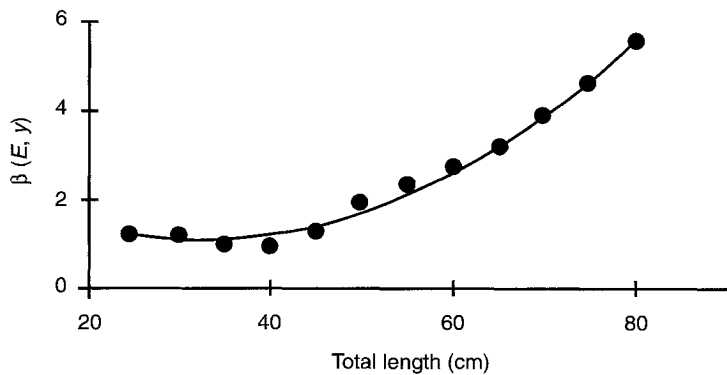
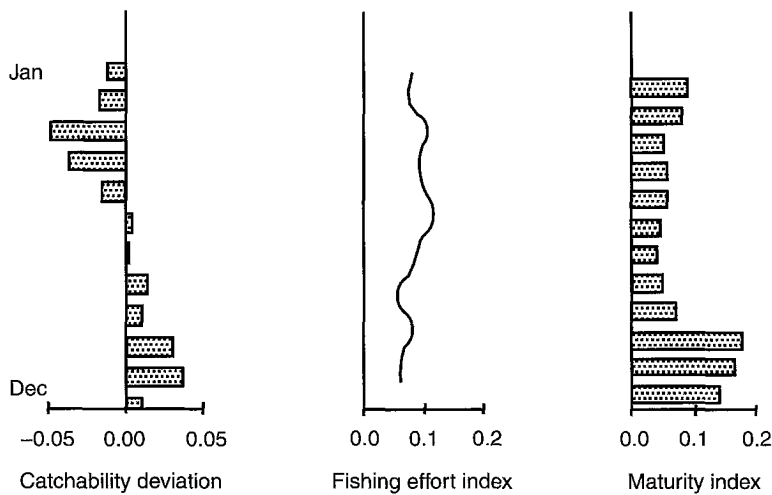
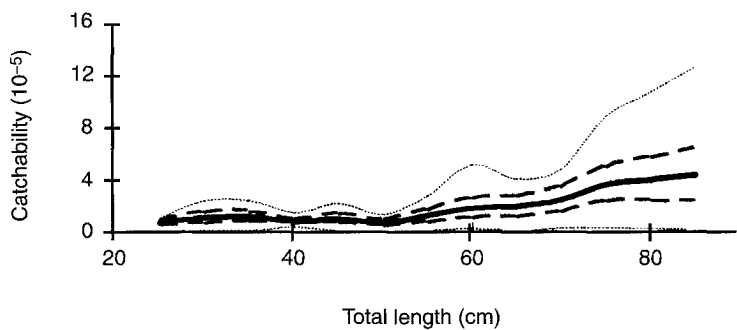
This approach was applied to the red grouper (*Epinephelus morio*, Serranidae) fishery from the Campeche Bank, Mexico. The main conclusion was that catchability is strongly associated with reproductive behaviour, particularly fish aggregations, with important differences between young and adult fishes (Fig. 1). The population abundance estimate was clearly different when density-dependent effects on catchability were considered (Fig. 2).

The same model was applied by Martínez (1993) to the sardine (*Sardinops caeruleus*) fishery in the Gulf of California, Mexico. Catchability patterns were well described and trends suggest that the fishery collapse could have been prevented (Fig. 3).

Conclusions

The catchability coefficient is a parameter reflecting the efficiency of fishing. It gives a measure of the quality of the fishing gears and the fishing fleets and the fishing strategy

Fig. 1. Catchability patterns resulting from the application of the integrated catchability model proposed by Arreguín-Sánchez (1992) to the red grouper (*Epinephelus morio*) fishery of Campeche Bank, Mexico. Top: catchability-at-length showing the average pattern (bold), the limits of one standard deviation (dashed bold lines), and the absolute minimum and maximum values (thin dashed lines) for a 15 year period. Middle: relationship between monthly departure of the catchability-at-length pattern (from the average), the index of fishing effort and maturity of fish. It illustrates the effect of the reproductive aggregation on fish vulnerability. Bottom: density-dependence effect on catchability with fish size, showing a constant effect on immature fish, increasing with size after maturity (first maturity length $L_m = 50$ cm TL).



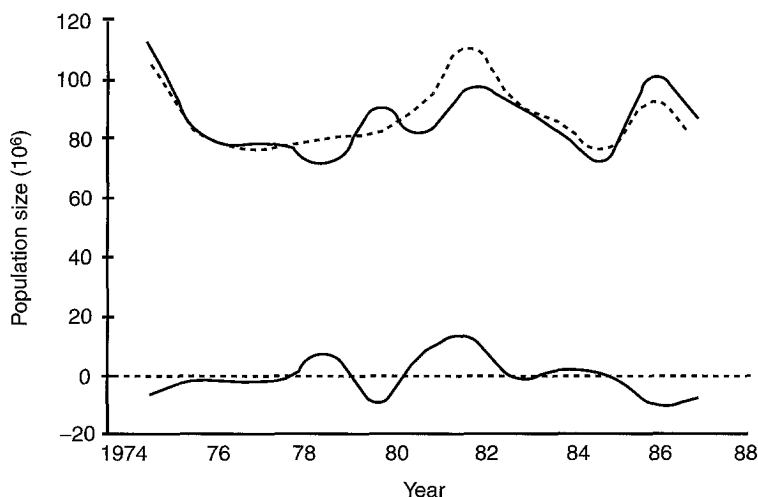
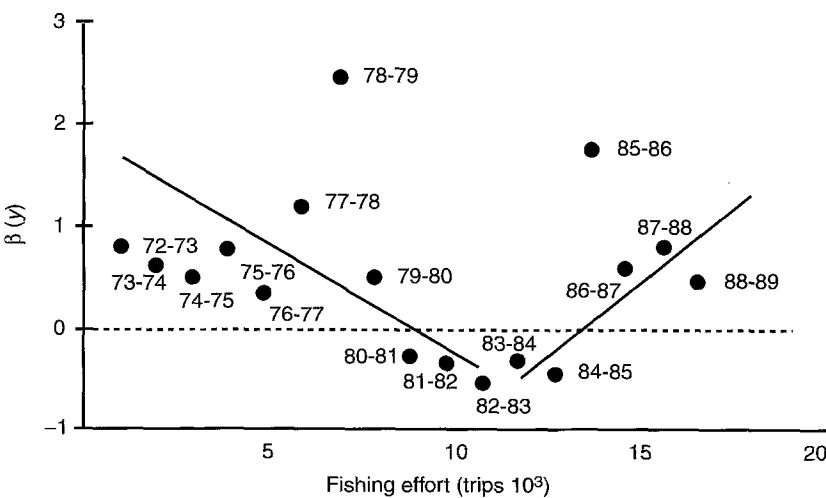
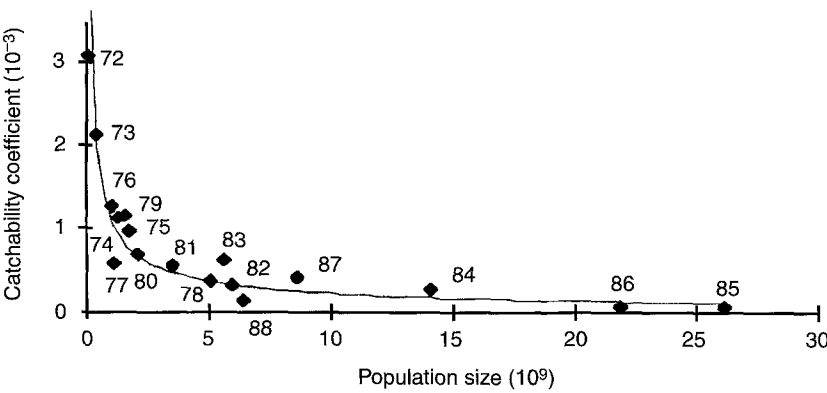
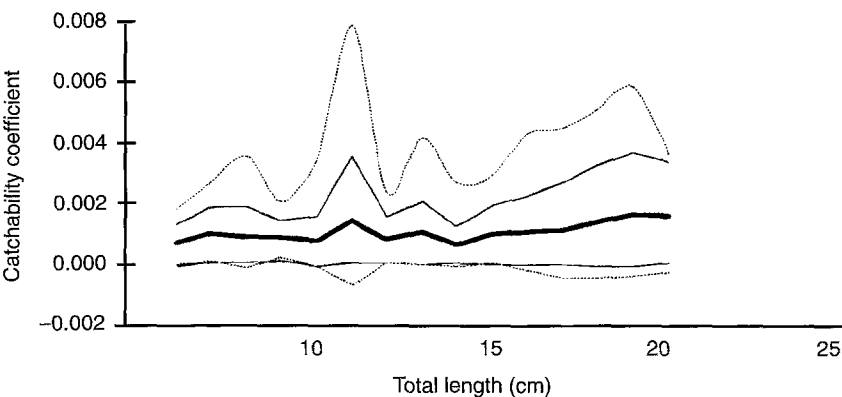


Fig. 2. Estimated population size of the red grouper (*Epinephelus morio*) fishery from Campeche Bank, Mexico. Top: when a density-dependent catchability effect is considered (bold), with respect to estimation in the absence of a density-dependent effect (dashed). Bottom: difference between both estimations above.

adopted, from knowledge of fish behaviour. In turn, fishing efficiency reflects fish mortality, which is a key parameter in regulating the sustainability of the fishery.

It is well recognized that catchability cannot be assumed constant but varies after various sources. These sources are associated with abundance, fish behaviour, population biology including its dynamics, quality and amount of fishing effort, fishing strategy and environmental conditions, among others. All these interacting factors are reflected in the catchability coefficient. Patterns have proven to be important in fishery behaviour as many have shown an inverse relationship between stock abundance and fishing effort.

Fig. 3. Catchability patterns from the application of the integrated catchability model (Arreguín-Sánchez, 1992) to the sardine (*Sardinops caeruleus*) fishery in the Gulf of California, Mexico (from Martínez, 1993). Top: catchability-at-length pattern showing the average trend (bold), the limits of one standard deviation (thin) and the absolute minimum and maximum values (dashed) over 20 years. Middle: inverse relationship between catchability coefficient and population size. Bottom: trend of $\beta(y)$, the rate of change of catchability with length with respect to equilibrium (see Equation 17), as a function of the fishing effort. Negative values indicate higher abundance and vulnerability of young fishes. For the fishing seasons 1980–81 to 1984–85, a large amount of small fish was caught; population decreased and catchability increased. Because fishing efficiency increased, fishing effort was also increased for the next fishing seasons, where small fish were less abundant. Population size decreased, from 1986 to 1987, more than 50%, and from 1985 to 1988 to 20%; while fishing effort increased almost 200%, and for the early 1990s, the fishery was collapsed. In the appropriate time, this analysis could have prevented the collapse of the fishery by controlling fishing effort at the levels found in the mid 1980s; that means, positive points corresponding to the 1985–86 to 1988–89 fishing seasons should be on the left side of the figure, corresponding to a fishing effort of less than 10^3 trips.



In the past, catchability was assumed to be dependent on one single factor; the identification of this key factor was based on previous personal experiences. A more thorough analysis of fishery behaviour has indicated the need to consider and evaluate the various sources of variation in catchability and integrate them in a comprehensive catchability coefficient. This approach will produce a more accurate estimation of catchability coefficient, fishing mortality and population size, for which the implications on fisheries management cannot be overlooked.

Summary

Catchability is a concept in fishery biology which reflects the efficiency of a particular fishery. Its quantitative magnitude is expressed by the catchability coefficient, which relates the biomass abundance to the capture or fishing mortality. This paper is a comprehensive review of catchability including the development of our knowledge, interpretation and estimation.

Catchability patterns indicate that the catchability coefficient has been used in two main lines: (a) increased efficiency of fishing effort and (b) its relation to population fishery processes for assessment and management purposes. It involves various aspects of the fishery, such as individual and population biology, characteristics of the fishing gear, amount of fishing, fishing strategies, and environmental fluctuation, among others.

The concept is proposed of an integrated model of the catchability coefficient, which incorporates various of the aspects mentioned above. It is illustrated with two examples of its application: the red grouper (*Epinephelus morio*) fishery from the Campeche Bank, Gulf of Mexico, and the sardine (*Sardinops caeruleus*) fishery from the Gulf of California.

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