

III.ii. Application of fish behaviour knowledge for improved assessment and fisheries management

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Consequences of fish behaviour for stock assessment

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The influence of fish behaviour on the most common stock assessment methods is reviewed. Fish behaviour may be divided into four major groups: habitat selection, aggregation pattern, avoidance reactions, and learning. Examples of temperate and tropical species are presented.

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Introduction

Indirect stock assessment techniques have improved considerably through the development of population dynamics, and the use of computers and adequate statistics have increased their precision. Direct stock assessment methods such as fisheries acoustics are still improving, largely because of benefits from technological progress.

Although fish behaviour is not directly represented through parameters in the stock assessment methods, there is an increasing awareness that behaviour is a major limiting factor in the accuracy of abundance estimates. To illustrate the reasons behind this awareness, we review how fish behaviour, grouped into habitat selection, aggregation patterns, avoidance reactions and learning, may influence the most common stock assessment methods (Table 1).

Habitat selection

Habitat selection is one of the functional behavioural systems for adult fish (Huntingford, 1986). Many fishes change habitat diurnally, seasonally, and some from year to year. Such changes in fish distribution can affect stock assessment.

Availability

A difficulty for direct stock assessment arises when fish occupy habitats unavailable to sampling gears. Acoustic assessment requires that fish be distributed from a few

metres below the surface to a small distance off the bottom (Mitson, 1983). Several economically important species such as cod (*Gadus morhua*) and walleye pollock (*Theragra chalcogramma*) live semipelagically, and in such cases a combination of acoustic and trawl surveys is applied (Godø, 1990; Wespestad and Megrey, 1990). A substantial difficulty for this approach is that semipelagic species sometimes choose to live mostly demersally or pelagically (Godø, 1990). Similarly, species usually living pelagically, such as herring (*Clupea harengus*), may distribute themselves in some instances so close to the surface or bottom as to be inaccessible to acoustic assessment (Jakobsson, 1983).

Short-term variation

Short-term variation in fish distribution makes it impossible to obtain the same observation in the same place at two different instants. Gerlotto and Petitgas (1991) observed that the biomass estimated by echo integration could double between two successive recordings of the same transect owing to movements of schools. Apart from generating a random process in the data set, such variability makes use of geostatistics difficult owing to the presence of highly different density values at the same geographical point. It may also put a limit on increasing the precision of an estimate by higher sampling intensity (Aglen, 1989). When the variability between two neighbouring transects is the same as that between two repetitions of a transect, no benefit can be expected by further decreasing the intertransect distance.

Table 1. Relative importance of four behavioural patterns on four categories of stock assessment approach.

Behavioural pattern	Stock assessment method			
	Cohort analysis, VPA, etc.	Surplus production models	Trawl survey	Acoustic survey
Habitat Choice				
Short term	0	0	+ or -	++ or --
Diurnal	0	0*	++ or --	++ or --
Seasonal	0	0*	++ or --	+ or -
Yearly	+ or -	+++ or ----	++ or --	0
Aggregation	0	+++ or ----	++ or --	++ or --
Avoidance	0	0	---	--
Learning	-(?)	-(?)	-(?)	0

0 = no influence of behaviour.

+, ++, +++ = increasing risk of over-estimation.

-, --, ---- = increasing risk of under-estimation.

* except if interannual changes in the fishing pattern are not taken into account.

(?) importance not clearly assessed.

Data gathered by trawl surveys generally also provide a high variability (Ulltang, 1977) which may partially result from horizontal or vertical displacement of the biomass. Repeated trawling at the same place may suggest varying influence of factors such as temperature (Rijavec, 1971), internal waves (Caverivière, 1982), and light intensity. Flatfishes may take advantage of tidal currents for horizontal migration by moving up in the water column when the flow direction is favourable (Arnold *et al.*, 1990), and the catchability may change accordingly.

Diurnal variation

In coastal areas, pelagic fish often display diurnal horizontal migrations. Menhaden (*Brevoortia patronus*) move inshore and on the surface at night, but are found offshore and close to the bottom during the day (Kempermer, 1980). Gerlotto and Petitgas (1991) observed that fish were present in the central part of the Gulf of Cariaco (Venezuela) by night and near the coast by day.

Clupeoids usually perform diurnal vertical migrations that seem mainly related to a light intensity preferendum (Blaxter and Hunter, 1982). Carangids of tropical areas also undertake vertical migrations, but this pattern is not constant and changes according to age and region (Boély and Fréon, 1979). In the Senegalese purse seine fisheries some species are caught during the day, others at night, and the catch per unit of effort (c.p.u.e.) therefore gives different abundance indices for different categories (day, night, day + night) of computation.

The proportion of species studied may vary diurnally as some demersal ones become pelagic by night. This change in behaviour may introduce biases to results from direct methods when sampling is conducted during both day and night (Engås, 1991). Vertical movements

may affect the swimbladder volume, especially in physostomatous fish, and may have an impact on target strength (Blaxter and Batty, 1990).

Seasonal variation

Surveys are usually conducted during the same time of year to avoid bias arising from seasonal variation in fish distribution. If fish are migrating, bias may occur in acoustic estimates, but this can be corrected by taking account of the mean migration speed (MacLennan and Simmonds, 1992).

Interannual variability

Dramatic fluctuations in biomass may change the area occupied by pelagic stocks (e.g. of clupeoids) by a factor of 10 or more. For demersal stocks, the population explosion may be associated with a complete change of habitat. For instance, along the West African coast, *Balistes carolinensis* was until 1971 considered to be a not very abundant demersal species. Then this species started to colonize the pelagic system during the first years of its life, and in 8 years its biomass increased to 10⁶ tons (Caverivière *et al.*, 1980), although it is now declining to the level that prevailed before 1970. The demographic explosion of *Macroramphosus* sp. off Morocco in the 1970s presented a similar pattern (Belvêze, 1991). None of these stocks was exploited, and catch-based methods were obviously not adapted for assessment.

Social aggregation

Fish can distribute and behave individually, assemble socially in shoals, or swim synchronized and polarized in

schools (Pitcher, 1983) These behaviour patterns have a significant influence on sampling.

Density distribution

The aggregative behaviour of fish induces a large dispersion and skewness in the distribution function of echo integration data. This is especially evident when the fish assessed are schooling (Aglen, 1989). The confidence limits of biomass estimates obtained with classical statistics may therefore be large, but the first two moments (mean and variance) of the distribution function still seem finite, and the central limit theorem may apply. However, cases exist where the distribution function of the data sampled does not have these properties. In such cases an increase in sampling rate has a limited effect on the precision of the estimate. There are examples of acoustic surveys in tropical areas that resemble a Pareto distribution (Lévy, 1925) with infinite variance. In such cases the arithmetic mean does not give a good estimate of the population.

Buerkle and Stephenson (1990) found large variations in biomass estimates from repeated night-time acoustic surveys of herring in Chedabucto Bay, Nova Scotia, Canada, which they claimed were caused by great dynamics in the aggregations. Aglen (1989) showed that variability in acoustic survey estimates decreases with increasing degree of coverage. Vilhjálmsson *et al.* (1983) and Strømme and Sætersdal (1987) demonstrated good replicability of repeated surveys in northern and tropical areas, respectively.

Target strength

Social aggregation also affects the orientation of fish, resulting in a higher average target strength when schooling than when shoaling (Foote, 1980). A diurnal variation in target strength has been observed for caged cod, herring, and mackerel (*Scomber scombrus*) (MacLennan, 1990). The variation is especially large (about 5 dB) for mackerel owing to hydrodynamic constraints on this swimbladderless fish (He and Wardle, 1986). Therefore, different target strength values should be applied for daytime schooling and night-time shoaling, but the validity of cage measurement may be questioned as fish may polarize by day as well as by night when affected by survey vessels. However, for walleye pollock the *in situ* target strength was found to be 3 dB lower by night than by day (Traynor and Williamson, 1983).

Acoustic shadowing

The echo integration method is linear (Foote, 1983). However, in fish aggregations with a large vertical extent, substantial extinction of the sound energy emitted from an acoustic transducer can occur (Røttingen, 1976). By recording the attenuation in the bottom echo as a function of the vertical extent of herring shoals in a

Norwegian fjord, Toresen (1991) fitted equations to correct the fish density estimates for extinction. A solution to correct for extinction in aggregations with varying density is proposed by Foote (1990).

Catchability

Changes in stock abundance of pelagic species often occur without noticeable changes in catchability or with changes inversely proportional to the area occupied by the stock (Ulltang, 1976; Shelton and Armstrong, 1983). On the other hand changes in catchability may occur without change in abundance when long-term changes in the environment influence the aggregation pattern (Mangel and Breder, 1985). For pelagic stocks exploited by purse seiners, the usual c.p.u.e. is computed using the time spent searching for schools. Evidently in such cases c.p.u.e. is not a good abundance index. The mean catch per set in purse seine fisheries could be considered as an abundance index under the assumptions that the mean school size is related to the stock abundance and that the catch per set is proportional to the school size. These assumptions seem to be met in the Senegalese sardinella fisheries after the data set is filtered (Fréon, 1989).

Vessel avoidance

Modern survey vessels generate substantial low-frequency noise that has peak energy within the hearing range of teleosts (Mitson, 1989). This noise may elicit avoidance reactions that may drastically reduce the fish density that can be recorded by echo integration units underneath survey vessels (Olsen *et al.*, 1983). Recordings from a small independent vessel when a survey vessel passes close to it have shown density reductions ranging from 40% to 90% for shoaling herring in Norwegian fjords, and cod and polar cod (*Boreogadus saida*) in the Barents Sea (Olsen, 1990). Other studies on cod and haddock (*Melanogrammus aeglefinus*) revealed no, or just weak, avoidance reactions to survey vessels running at normal cruising speeds (Ona and Godø, 1990). Similar studies on tropical clupeoid species in shallow water showed no reduction in fish density during passage of small survey vessels, either when sailing or when motor driven (Fréon *et al.*, 1990). Schools of *Sardinella aurita* off Venezuela avoided vertically, but only in the upper 20 m, when a medium-sized survey vessel passed over them, and this resulted only in little underestimation of the density as the average tilt angle during the dive was estimated to be less than 10° (Gerlotto and Fréon, 1992). Recordings by sonar show about 20% underestimation of fish density owing to horizontal avoidance by herring schools in the North Sea, and no avoidance of spawning migrating capelin schools in the Barents Sea (Mísund 1991; Mísund *et al.*, 1992). This indicates that vessel avoidance reactions may vary substantially, and Neproschin (1979) argued that Pacific mackerel (*Pneumatophor-*

us japonicus) avoids most when well fed and swimming in schools, less when shoaling and feeding, and even less when occurring in low-temperature water. Herring seem to react less the better the sound propagation conditions, but more strongly when on spawning migration than when feeding or on feeding migration (Misund, 1991).

At night, avoidance may occur as a response to visual stimulation by the vessel's lights. Lévénez *et al.* (1990) observed vertical avoidance of tropical clupeoids off Venezuela during new moon when running a survey vessel with a 500 W light on the bridge, but the mean echo integral was the same with the lamp on or off. In a similar experiment, Gerlotto *et al.* (1990) observed no vertical avoidance, but found indications of species- or size-dependent horizontal avoidance when the lamp was on.

Vessel avoidance reactions may increase during trawling, as observed for cod and haddock (Ona and Godø, 1990), and such reactions may even make trawl sampling of schooling species such as herring difficult (Misund and Aglen, 1992). Similarly, vessel avoidance reactions may cause difficulties in combining the results from swept area and echo integration estimates of semipelagic fish. However, for Pacific whiting (*Merluccius productus*), Nunnallee (1991) observed no change in vertical distribution when a trawler passed over (but a strong avoidance of the trawl).

Fishing gear avoidance

A basic assumption of assessment methods is that samples by trawl are representative of the populations recorded. There is increasing evidence that this sampling principle is an oversimplification, as gear avoidance reactions change according to species and age of the fish (Engås, 1991; Godø, 1990). Main and Sangster (1981) observed that cod search towards the bottom when approached by a bottom trawl, haddock rise and may escape over the headline in substantial numbers, and whiting (*Merlangius merlangus*) tend to aggregate more in the middle of the trawl opening. The reactions of cod differ among size groups, so that the smallest fish escape under the ground gear and are grossly underestimated in the catches (Godø, 1990; Engås, 1991).

Gear avoidance seems mainly elicited by visual stimuli, and the reactions decrease at night-time (Glass and Wardle, 1989). However, endogenous rhythms may also be of importance because the catchability of demersal fish in West Africa increases suddenly before dawn, without a change in light intensity (Baudin-Laurencin, 1967).

Learning

Like all animal groups, fishes are able to adapt their behaviour towards fishing gear through learning (Fernø

and Huse, 1983). Pyanov (1992) argues that "one-trial learning" may exist because tagged fish were not caught any more by the trawl gear that caught them initially. Similarly, Soria *et al.* (this volume) showed that under certain conditions, experienced clupeoids can transmit avoidance behaviour to a naive school. This indicates that fish are able to learn, allowing them to avoid the fishing gears after having escaped once. Moreover, fish can retain their learned experience for months (Coble *et al.*, 1985).

The consequences of learning may be a long-term decrease in efficiency of the fishing gears, and biases in the use of c.p.u.e. as indices of abundance. If the oldest fish are more experienced with fishing gear, their fishing mortality may be lower than expected. This will affect VPA and cohort analysis because the fishing mortality of the oldest age groups must be estimated *a priori*, and the corresponding error in this estimation will propagate in the vector of mortality.

Conclusion

All stock assessment methods considered here may suffer biases owing to fish behaviour (Table 1). Cohort analysis must be tuned by at least one parameter (fishing effort, recruitment, c.p.u.e.) estimated by other methods, and may thereby be biased. Stock assessments based on fishery-independent, *in situ* observations are becoming increasingly important, and on such methods (fishery acoustics, trawl surveys) variations in natural fish behavioural patterns and in reactions to vessels and fishing gear may have large impacts. In order to understand the determinism of natural behavioural patterns and avoidance reactions, we argue that fish behaviour research must be escalated with special attention to *in situ* studies, as there is a large potential for increasing the accuracy of stock assessment methods through a better knowledge of fish behaviour.

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