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Contemporary management issues confronting fisheries science

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Abstract

Stock collapses have occurred worldwide. The most frequently cited cause is over-fishing, suggesting that fisheries management has been ineffective in controlling exploitation rates. The progression of a fishery from an over-exploited to a collapsed state involves impairment of the reproductive capacity of the target species, i.e. recruitment over-fishing. In many cases, this occurs by reduction of the spawning stock biomass (SSB) through the systematic elimination of spawning components within a stock complex. While operational definitions of minimum levels of SSB have been developed, they have seldom been applied and never adopted in a Canadian groundfish management context. The answer to the question of how much is enough to perpetuate a stock under exploitation has been illusive. Serebryakov [J. Cons. Int. Explor. Mer, 47 (1990) 267] has advocated definition of critical levels of SSB based on survival rates (R/SSB). We review his method and discuss the utility of the approach. An alternative approach to the problem of estimating minimum SSB is through a fundamental revision of the traditional stock and recruitment relationship. Explicit theoretical SSB thresholds below which reproduction/recruitment is severely impaired based upon density-dependent mating success (or Allee effects) is considered a superior approach to the question of how much is enough because of its ecological grounding. However, the successful application of this approach will require re-definition of the space/time scales of the management unit. Finally, support is growing for the establishment of closed areas or “no-take zones” as an alternative approach to managing the problems of fishing a stock complex by enabling sub-populations to escape fishing. While the expected benefits of areas protected from fishing are numerous, clear demonstrations of benefits of such areas in marine temperate ecosystems are lacking. In fact, unintended negative consequences may result from such actions. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

Teleost fish represent the only major food source harvested from natural populations. This has necessitated that they be managed with explicit goals and objectives in order to sustain harvests. While this

appears to be a logical approach to the conservation of renewable resources, it is a relatively modern phenomenon. For example, limits on total allowable catches (TACs) in the Northwest Atlantic were first introduced in the 1970s, well after record high groundfish landings and stock collapses occurred during the 1960s (Scott and Scott, 1988). In the North Sea, catch quotas were first implemented in the mid-1970s (Daan, 1997).

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Table 1

The relevant science needed to address various fishery management issues. Note that one or more science components may be needed to address a particular issue

Fishery Management Issue	Relevant Science
Definition of management unit/ area for the target species	Population regulation theory; density dependence; density independence
Setting of limits on catches (quotas)	Stock and recruitment
Prevention of: recruitment overfishing; growth overfishing	Population structure/stock discrimination; genetics; meristics; otolith chemistry
Discarding of immature fish and non-target species	Species distribution/ migrations; community ecology
Managing mixed-population fisheries (protection of spawning components or sub-stocks)	Theory of island biogeography; zoogeography/ biogeographical provinces; tropho-dynamics/ bioenergetics/trophic cascade
Definition of time/area closures	Metapopulation theory
Implementation of: precautionary approach; ecosystem approach	Behavioural ecology; prediction capability; climate variability/physical forcing
Protection of biodiversity	Risk analysis/dealing with uncertainty

Fisheries management makes some important biological assumptions. One of the key assumptions is that a relationship exists between fishing mortality and the sustainability of the fishery. If fishing mortality exceeds a certain limit the productivity of the resource is expected to decline and the stock may collapse. Regulation of fishing, therefore, is consid-

ered the manager's prime method of intervention. The usual regulations imposed to achieve this objective include setting limits on catches, closures of areas and times of fishing, restrictions on the kind of gear, and the allocation of catches to various sectors of the fishery.

While controlling exploitation rates is indeed a primary task of fisheries management, it is not the only issue and the list is growing (Table 1). Knowledge generated by scientific research can be used to make informed decisions about many of the issues. For example, definition of the management unit is greatly aided by information about the population structure and migration patterns, and the ability to discriminate the stock from adjacent populations. Managing mixed-population fisheries would benefit from a similar base of scientific knowledge. Setting of appropriate TACs depends, in part, on having an underlying theory of how the stock responds to fishing, a stock and recruitment relationship, and some knowledge of how climate variability influences stock productivity (Table 1). Implementation of the precautionary approach could potentially involve all of the relevant science listed in Table 1. Unfortunately, scientific information has only played a limited role in the management of fisheries, particularly in stock assessments where much of the relevant knowledge from research carried out on fish population dynamics remains unused (Sherman, 1991; Ulltang, 1998). Also, the underlying models are considered an over-simplification of the complex dynamics of marine ecosystems (McGlade, 1999).

It should come as no surprise that fisheries have

Table 2

Magnitude of the decline in spawning stock biomass for Canadian Atlantic cod stocks that collapsed during the early 1990s. Current status of the stock and associated fishery are also indicated

Location	M.U. (NAFO Division)	% Decline in SSB	Year of Moratorium	Stock/Fishery Status in 1999
Labrador and northeast Newfoundland	2J3KL	98.6	1992	Closed (offshore); partial recovery and limited fishery (inshore)
Southern Grand Bank	3NO	91.2	1993	Closed
St. Pierre Bank	3Ps	77.0	1993	Partial recovery and limited fishery
Northern Gulf of St. Lawrence	3Pn4RS	94.7	1993	Partial recovery and limited fishery
Southern Gulf of St. Lawrence	4TVn	88.6	1993	No recovery and limited fishery
Eastern Scotian Shelf	4VsW	84.5	1993	Closed

generally not been managed successfully. From a Canadian Atlantic groundfish perspective, several cod (*Gadus morhua*) stocks have been severely over-fished and reductions in spawning biomass range from 77 to 99% of the historical maximum (Table 2). Fishing moratoria were imposed in the early 1990s in all affected cod management units to counteract these declines. Yet, to date, there are no significant indications of recovery with the possible exception of cod along the south coast of Newfoundland in NAFO Div. 3Ps. In his review of the collapse of ten major fisheries for small pelagic marine species, Beverton (1990) noted that only one stock has fully regained its original size and Icelandic spring-spawning herring (*Clupea harengus harengus*) has failed to reappear after 20 years. In a literature review of the causes of stock collapses (mainly Atlantic and Pacific herring) that have occurred worldwide, Pearson et al. (1999) have shown that the most frequently cited cause was over-fishing. In the North Sea, TAC management of the flatfish fisheries has created more problems that it has resolved and current fishing mortality rates on plaice and sole stocks are at an all-time high (Daan, 1997). Nehlsen (1994) identified over 200 native Pacific salmon stocks, distributed throughout Washington, Oregon, Idaho and California, whose future persistence was in doubt. Nearly half of the identified stocks were considered to be at a high risk of extinction. Over-fishing and habitat degradation was cited as the leading causes. Cury and Anneville (1998) give many more examples that extend the list of collapsed marine fish populations resulting from intense exploitation. Fisheries ecologist should not take this news too hard as other animal groups are faring no better for somewhat similar reasons. For example, among avian taxa currently endangered by extinction, 82% are associated with habitat loss, 44% by exploitation, 35% by introductions, and another 12% by pollution or natural events (Boyce, 1992). It is obvious that one of the most difficult things to do in the management of natural resources is to keep exploitation pressure in check.

2. The failure of collapsed stocks to recover

When fishing is greatly reduced or eliminated, as was the case for many cod stocks in the Northwest

Atlantic (Myers et al., 1997) and the small pelagic species discussed by Beverton (1990), full recovery was expected. The fact that this has not occurred in these cases suggests the effects of over-fishing may not be reversible. Numerous other examples exist as well of failed recovery (Hutchings, 2000). Stock recovery may be impeded for a variety of reasons. They may remain perpetually over-exploited due to multi-species harvesting technology (Caddy, 1999a). As the fishery and market shift targets to lower valued species, the original target species is captured incidentally as by-catch. This could put the depleted species in a position where stock recovery is difficult to achieve. The effects of fishing on the marine habitat, such as disturbance to the seabed and consequent damage to benthic organisms, may reduce its productivity capacity (e.g. Watling and Norse, 1998; but see Pastoors et al., 2000 for a counter argument). Further, some have suggested that due to environmental changes, stocks may collapse irrespective of a conservative management approach (Sinclair et al., 1996; Gullestad, 1998). Despite biblical precedence, the question of how much is enough to perpetuate a population has never been defined. Even though most fishery management plans include concerns for minimum spawning stock biomass levels necessary for future recruitment, there exists no operational definition (Sinclair et al., 1996). Finally, the potential exists for fishing to have a major impact on a population's genetic or spatial structure (Hilborn, 1985; Hilborn et al., 1995). It is these latter two concerns that form the basis for the remainder of the paper. But first we will review some fundamental concepts in population regulation theory.

3. Population dynamics of exploited species

It has generally been assumed that the path to extinction can be reversed if fishing mortality has been reduced sufficiently or eliminated. This is predicated on the existence of compensatory population dynamics where the recruitment (or survival) rate (R/SSB) increases as the population declines. In turn, this compensates for reductions in egg production associated with decreasing spawning stock biomass. The compensatory response is embodied in the well-known Ricker and Beverton and Holt stock

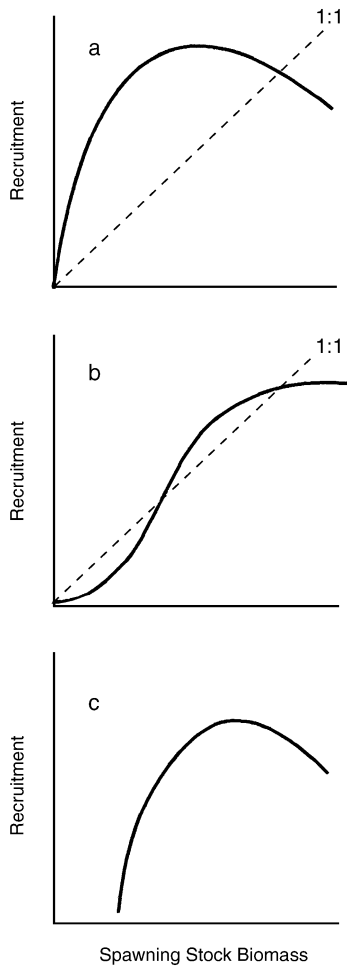


Fig. 1. Illustration of three types of stock and recruitment relationships: (a) the commonly observed compensatory relationship, (b) the uncommon dependensary relationship, and (c) the non-zero intercept model incorporating the Allee effect.

and recruitment models (Fig. 1a). A recent study utilizing stock and recruitment data for 100 + commercially exploited fish stocks worldwide, concluded compensation is the most common form of population regulation in marine fishes and that the effects of over-fishing are reversible (Myers et al., 1995). Interestingly, two collapsed cod stocks in the northwest Atlantic that have failed to recover despite several years of fishing moratoria, conform to the compensatory model (Fig. 2). The failure of collapsed stocks to recover suggests that other mechanisms are influencing the production dynamics at low population levels.

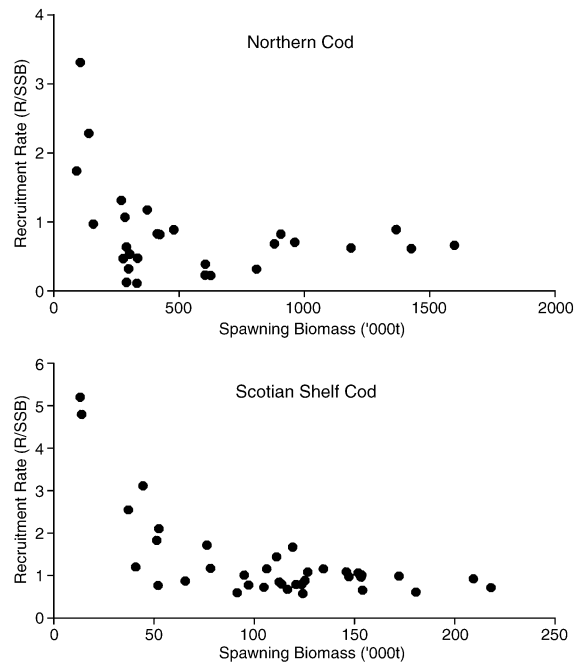


Fig. 2. Examples of some fish stocks conforming to the compensatory response. Recruitment (or survival) rate (R/SSB) is plotted against spawning stock biomass (SSB) for Northern cod (NAFO Div. 2J3KL) and Scotian Shelf cod (NAFO Div. 4VsW). These stocks collapsed in the early 1990s and despite the cessation of fishing for several years have not yet recovered.

An apparently much less common form of population dynamics, but one consistent with the lack of recovery of collapsed stocks, is dependensary population dynamics. In this model recruitment rate decreases (or mortality rate increases) at low spawning stock levels. A stock and recruitment relationship encompassing a dependensary response has a concave shape near the origin and a second, lower equilibrium point that is unstable (Fig. 1b). If the stock is reduced to levels below this secondary equilibrium it will collapse. Nearly all discussion of dependensary mechanisms in the fisheries literature concentrates on predation. For example, when a predator consumes a constant number of prey, the percentage of the prey population lost to predation increases as the population declines and this mechanism has been supported by empirical studies (see review in Liermann and Hilborn (1997).

Two recent studies (Liermann and Hilborn, 1997; Shelton and Healey, 1999) have suggested that

depensatory population dynamics may not be as infrequent as previously suggested by Myers et al. (1995). The former authors argue that depensation is difficult to detect because of limited and variable data associated with low spawning stock sizes and cautioned that not allowing for the possibility of depensatory dynamics is ill-advised. Oddly, a major assumption associated with both the compensatory and depensatory stock and recruitment relationships is that the curve should pass through the origin, despite the lack of data at low population levels. Larkin (1978) put a somewhat different spin on things when discussing the fitting of theoretical models to stock and recruitment data. He stated that “It is common gossip that if you did not have the certain knowledge that zero adults produce zero offspring, you could fit a Ricker model, or a Beverton–Holt model, or a straight line, or a circle with equal satisfaction”. However, it has been established in other animal populations that threshold population levels must be exceeded before successful reproduction can occur (Courchamp et al., 1999). Therefore, while it is true that zero adults produce zero offspring, it is also possible that a threshold exists in marine fish populations below which a population cannot reproduce.

A stock and recruitment relationship with an explicit SSB threshold (i.e. a non-zero intercept) is depicted in Fig. 1c. This relationship is intended to convey the Allee effect, defined as decreased reproduction in a species when their population numbers are reduced or rare. Allee (1931) was concerned with physiological and behavioral effects and contended that under-crowding or lack of aggregation as well as over-crowding was limiting to population growth and survival. While most are familiar with examples associated with the latter effect, the former one has been less well studied. Several mechanisms have been hypothesized to cause the Allee effect. Social interactions necessary for reproduction may be lacking or it may be difficult to find a mate when population numbers are low. Decreased reproductive success (egg fertilization) and/or a breakdown in social structure and migration patterns may occur at low spawning densities. Difficulty in fending off predators or competitors and a requirement for critical population numbers to be exceeded before food resources can be properly exploited are also possible mechanisms (Asmussen, 1979; Dennis, 1989; Boyce, 1992).

Some species where Allee effects have been demonstrated or hypothesized to exist include abalone (Davis et al., 1996; Babcock and Keesing, 1999), Pacific sardine and Downs herring (Gomez-Munoz, 1995), passenger pigeon (Halliday, 1980), sea urchins (Quinn et al., 1993), flour beetles, ship ticks and muskrats (Asmussen, 1979), and whooping cranes and butterflies (Wells et al., 1998). Further examples are given in recent reviews by Courchamp et al. (1999); Stephens and Sutherland (1999). With the exception of recent work by Ludwig (1998); Frank and Brickman (2000), the incorporation of Allee effects (or “critical depensation”) in contemporary fisheries science has been lacking.

4. Minimum spawning stock biomass — how much is enough?

The question of how much of a stock needs to be protected in order to maintain its reproductive capacity has been widely debated within the scientific community. Protection of the spawning stock is a widely held conservation objective commonly referred to as the prevention of recruitment over-fishing. Recruitment over-fishing occurs when a population has been fished down to a point where recruitment is greatly reduced. Because recruitment over-fishing generates stock collapse (Sinclair et al., 1996), our concern here is with defining the level of adult abundance, from both an empirical and theoretical standpoint, required to prevent this effect.

4.1. Serebryakov's method

An empirical method for defining operational targets of minimum SSB was devised by Serebryakov (1990). He argued that the assessment of recruitment (or survival) rates (R/SSB) was a possible way to search for factors that lead to the occurrence of strong, average or poor recruitment at various spawning stock biomass levels. He originally proposed definitions in terms of fecundity but they can be translated into terms of biomass as was done by Maguire and Mace (1993) in their search for biological reference points for Canadian Atlantic gadoid stocks. Three threshold levels were identified: (i) Safe spawning stock biomass — biomass at which average survival gives a strong year-class. It is calculated by dividing the

Table 3

Biological reference points for some Canadian Atlantic gadoid stocks (from Maguire and Mace, 1993). Critical levels of SSB ('000 t) derived by the method suggested by Serebryakov (1990) were compared to the estimated SSB for the most recent year available (in parentheses) at the time of the analysis. Stocks in bold were considered to be at dangerously low levels of SSB. Stock status in 1994 is shown in the final column

Stock	Spawning Stock Biomass ('000 t)				Status in 1994
	Safe	Minimum	Dangerous	Recent	
2J3KL Cod	388	291	89	70–110 (1991)	Collapsed
3Ps Cod	100	80	41	76 (1990)	Collapsed
3Pn4RS Cod	175	154	80	55 (1992)	Collapsed
4TVn Cod	116	93	23	114 (1992)	Collapsed
4VsW Cod	61	53	20	27 (1991)	Collapsed
4X Cod	70	59	24	84 (1991)	o.k.
5Zj,m Cod	57	42	14	41 (1991)	o.k.
4VW Haddock	53	33	8	19 (1985)	Collapsed
4X Haddock	61	52	16	23 (1987)	o.k.

abundance of a strong year-class by the mean survival rate. (ii) Minimum spawning stock biomass — biomass at which average survival gives an average year-class, high survival gives a strong year-class and low survival gives a poor year-class. It is estimated by dividing the abundance of an average year-class by the average survival. (iii) Dangerous spawning stock biomass — biomass at which high survival is required to produce an average year-class. It is estimated by dividing the abundance of an average year-class by the highest survival rate.

At a “Risk Evaluation and Biological Reference Points for Fisheries Management” workshop held in Halifax (November 1991), Maguire and Mace (1993) estimated the Serebryakov thresholds for eleven

groundfish stocks in the Canadian Atlantic. They used data input from analytical assessments to calculate the thresholds, although survey data alone could be used for this purpose. In addition, Maguire and Mace (1993) used the 75th percentile of the distribution of year-class sizes to approximate the abundance of a strong year-class. Some of their results are reproduced in the Table 3.

At the time of their analysis and based on a comparison with recent estimates of SSB, it was concluded that five out of nine stocks (2J3KL cod, 3Pn4RS cod, 4VsW cod, 4VW haddock, and 4X haddock) were at dangerously low levels (Table 3). Two other stocks (3Ps cod and 5Zj,m cod) were at minimum levels and the remainder were considered “safe”. As it turned out a few years later, four of the five stocks considered to be at dangerously low levels collapsed and were placed under fishing moratoria. An example of this method using assessment data for Northern cod is shown in Fig. 3. It is not clear why the Serebryakov thresholds for the Canadian Atlantic groundfish stocks did not generate any management action. In retrospect, the thresholds appeared to correctly classify those stocks in danger of collapse. One possible explanation for ignoring these reference points may have been the reluctance, at the time, to assume any relationship between recruitment and spawning stock biomass. At the same workshop, O’Boyle (1993) claimed that the analysis of stock and recruitment relationships had proven to be exceedingly difficult and therefore such models were not extensively used in the management of marine fish populations.

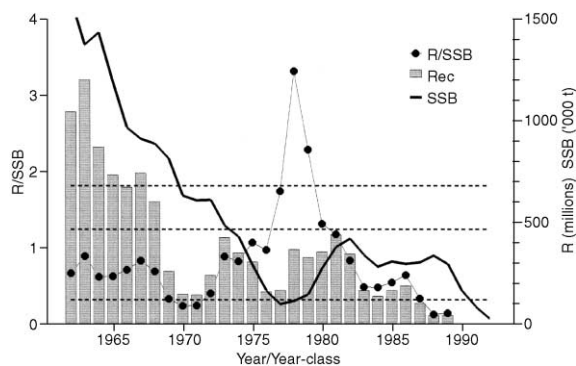


Fig. 3. Application of the Serebryakov method, as modified by Maguire and Mace (1993), to Northern cod. Horizontal dashed lines from top to bottom show safe, minimum, and dangerous spawning stock biomass thresholds.

Somewhat similar points have been raised before (Larkin, 1978; Peters, 1991; Koslow, 1992). However, a point has been reached in many fisheries where stock sizes have been reduced to levels where S–R relationships have taken on great importance.

Some improvements to the Serebryakov method, as modified by Maguire and Mace (1993), are obvious. SSB in all but one of the stocks examined was based on a constant knife-edge maturity ogive. Maturation is more likely to be spread over several ages and maturity schedules have probably changed over time. Therefore additional work on defining suitable maturity ogives is warranted. Furthermore, there is evidence that fecundity is not a simple function of weight — larger fish produce more eggs per unit weight than smaller fish. Differences also exist in the viability of eggs and larvae produced by first time versus repeat spawners (see Dutil et al., 1998). Ideally, annual estimation of fecundity would satisfy many of the concerns raised about the method; however, such estimates exist for very few stocks (Serebryakov, 1990; Marshall et al., 1998). A potential drawback of the Serebryakov reference points is that they are temporally variable and may change with the addition of data from new stock assessments. More importantly, the method ignores stock structure, and the derived thresholds, which are based upon stock and recruitment data at the management unit scale, are certain to be well beyond the levels applicable to individual sub-stocks.

4.2. Other thresholds

All theoretical stock and recruitment models share one common assumption, i.e. the curve passes through the origin. This logical necessity has probably done more harm than good. History has shown that it is quite possible for a species to be doomed to extinction even when it still appears to be quite abundant (e.g. see Quammen, 1996 for a sobering account of the extinction of the passenger pigeon). Conservation biologists have been thinking about criteria for what constitutes a viable population as well as the minimum number of individuals of a species that constitutes a viable population (Shaffer, 1981). These thoughts have been embodied in a loose, quantitative analysis framework known as population viability analysis (PVA) and minimum viable population

analysis or MVP (Boyce, 1992). PVAs are somewhat analogous to analytical stock assessments. They are generally population analyses or simulations that require some understanding of the population regulation mechanisms of the species and they depend upon the extent of available data as well as the expertise of the modeller (Boyce, 1992). PVA provides an estimate of how long a population will persist assuming that the ecological processes operating during the historical (or reference) period remain intact and unchanged in the future. An MVP is an estimate of the number of organisms of a particular species that constitutes a viable population and, in a fisheries management context, an MVP would represent a limit reference point (*sensu* Caddy, 1999b). Time and space persistence criteria for a given species contribute to an MVP estimate and there are some components of viability analysis that establish fixed thresholds below which MVPs should not drop (Soule, 1987). Unfortunately, sufficient data are rarely available to derive reliable estimates for all of the parameters necessary to determine an MVP and how well ecologists can predict future population trends over long time scales is questionable (Boyce, 1992). Fisheries scientists are all too familiar with failed attempts to model and forecast population trends (Walters and Maguire, 1996).

Boyce (1992) argues that the ultimate causes of extinction are primarily ecological and that certain aspects of ecology such as density dependence, spatial heterogeneity, and the Allee effects are of particular importance because they have major consequences to the probability of extinction. Allee effects are particularly important because these mechanisms create thresholds below which extinction is highly probable. While Allee effects have been postulated to occur in a broad diversity of taxa, a lack of empirical evidence weakens support for its existence. However, adoption of a precautionary approach dictates that we need to be concerned about Allee effects as a possibility and that it be examined closely. Interestingly, a stock and recruitment relationship recently developed for southern Australian abalone exhibited a positive x -intercept (Shepherd and Partington, 1995). The authors suggested that this was evidence for the Allee effect and considered that adult densities falling below the empirically derived threshold would be associated with recruitment failure and ultimate collapse of the

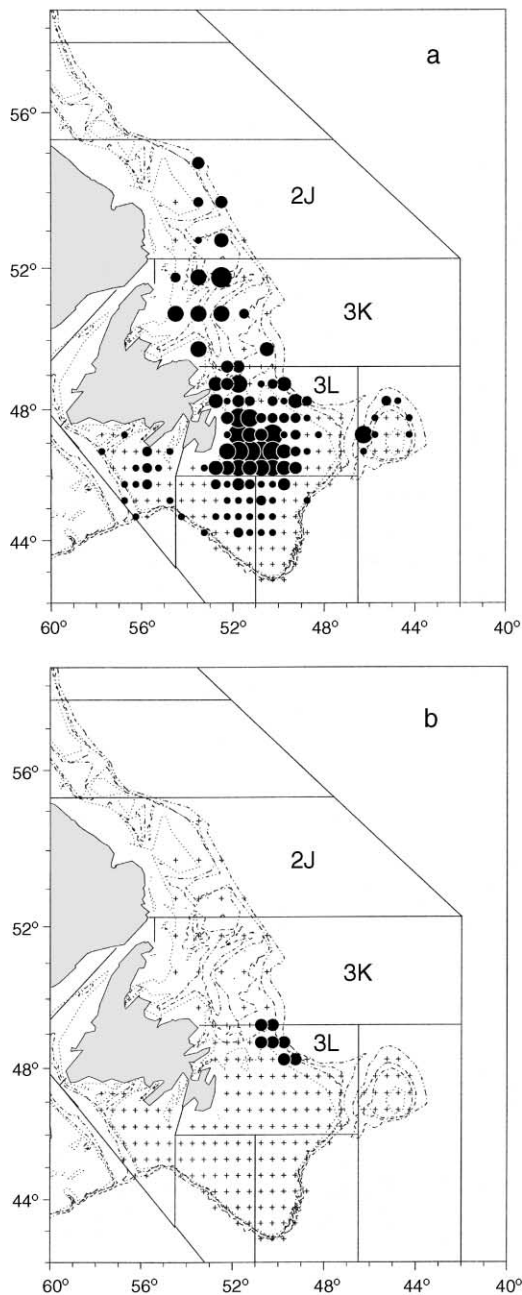


Fig. 4. Erosion of sub-stock structure of Northern cod in NAFO Div. 2J3KL. (a) Locations of cod spawning during the period 1948–1992 (adapted from Hutchings et al., 1993). (b) Locations of cod spawning during the period 1990–1993 (adapted from DeYoung and Rose, 1993).

stock. It is important not to be constrained by theoretical expectations and as Frank and Brickman (2000) have recommended — a null recruitment model with a non-zero intercept should be examined routinely in stock assessments.

In a fisheries management context, meaningful definition of population thresholds and their successful application will require changes to the space/time scales of the management unit in order to account for sub-stock structure.

5. Population structure

5.1. Erosion of intra-specific diversity

It is widely recognised that many stocks have a complex structure composed of spawning components or sub-stocks within a management unit that may have different productivities (e.g. in terms of survival and growth rates). For example, reproductively isolated sub-stocks have been identified within the Northern cod stock complex. This has been supported by meristic, genetic and tagging studies (Templeman, 1981; Bentzen et al., 1996; Taggart et al., 1995). Spring and fall spawning components of cod have been reported from the eastern Scotian Shelf based on egg and larval surveys (Frank et al., 1994). Management units for herring typically contain several spawning components (Stephenson et al., 1999). Knudsen (1999) provided a dramatic example of the complex stock structure of Pacific salmon where the number of populations per management unit in Alaskan waters ranged from 13 to 48. Furthermore, fishermen's knowledge is an important source of information documenting the existence of complex population structure (Ames, 1998; Stephenson, 1999). Hilborn (1985) urged that fisheries scientist and managers of demersal, pelagic, and even freshwater fisheries should consider the implications of stock structure on the analyses of fishing policies.

The UN Convention on Biological Diversity defines sustainable use as “the use of components of biological diversity in a way and at a rate that does not lead to the long-term decline of biological diversity, thereby maintaining its potential to meet the needs and aspirations of present and future generations” (Tasker and Knapman, 1999). In a fisheries

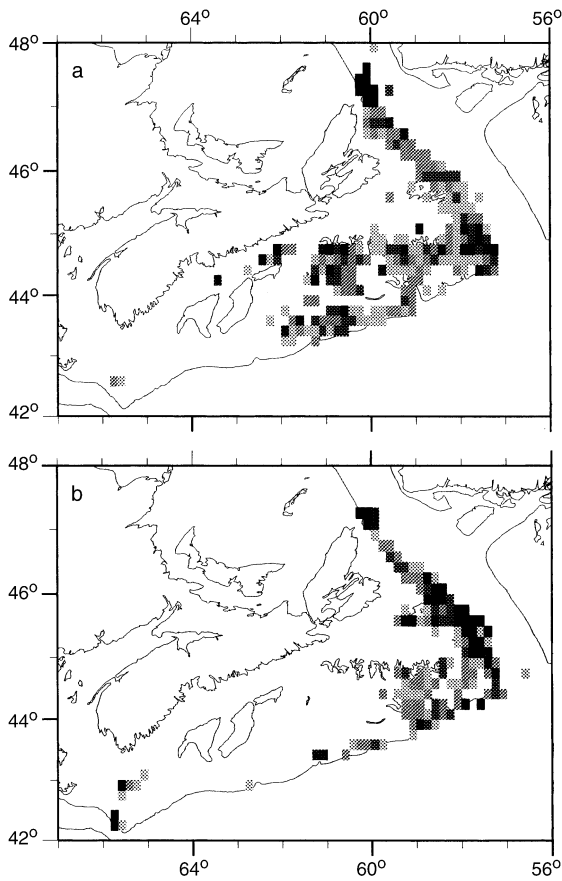


Fig. 5. Erosion of sub-stock structure of Scotian Shelf cod in NAFO Div. 4VsW based on the average catch rates of offshore trawlers (1 ton/h and greater) directing for cod, monitored by fisheries observers, during January to June. This type of information was considered a proxy for pre-spawning and spawning aggregations of cod. (a) Composite of data from 1979–1984. (b) Composite of data from 1988–1992. Intensity of shading is proportional to catch rates.

management context, this implies that a stock should be exploited in a sustainable manner with little or no adverse effect on biological diversity. It should be noted that in this context we are dealing with intra-specific diversity. Unfortunately, even at conservative exploitation levels, the possibility exists that fishing effort may be overly concentrated on individual spawning components within a stock complex leading to their demise (Sinclair et al., 1996).

Exploitation of cod spawning aggregations in the NW Atlantic was a very common practice resulting in a local (i.e. bank-scale) concentration of intensive fishing effort (Kulka et al., 1996). Two examples are

shown here illustrating the net effect of this practice. Historically, spawning locations of Northern cod were widespread and concentrated in the offshore shelf areas (Fig. 4a). Spawning concentrations were relatively high on Hamilton and Belle Isle Banks in Div. 2J, off northeast Newfoundland in Div. 3K, and within 100 km of the Newfoundland coast in Div. 3L (Hutchings et al., 1993). After the collapse of Northern cod in the early 1990s, the only offshore spawning concentration of cod occurred along the Div. 3K/3L boundary along the outer edge of the shelf (De Young and Rose 1993). The erosion of sub-stock structure within the Northern cod management unit appears to have been quite severe, with several sub-stocks evident prior to the collapse and only one or two thereafter (Fig. 4b). The second example deals with cod on the central and eastern portion of the Scotian Shelf which comprise a single management unit. Historically, during spring, large spawning concentrations of cod aggregated on the offshore banks of the central Scotian Shelf where offshore trawlers experienced exceptional catch rates (Fig. 5a). Just prior to the collapse of this stock, the fleet distribution (assumed to reflect spawning concentrations) shifted to the east, primarily in association with the edge of the shelf (Fig. 5b). The productivity of this stock, as well as that of Northern cod, continues to be quite low despite the existence of fishing moratoria since the early 1990s. Expectations for rapid recovery of these depleted stocks were high given the existence of compensatory population dynamics (Fig. 2). We believe these failed expectations are rooted in the primary assumption underlying all stock assessments, i.e. the stock under consideration represents a unit stock (Dickie, 1979).

5.2. Some things that happen when the unit stock assumption is violated

Dickie (1979) warned that uncritical application of the unit stock concept can obscure the understanding of a number of production features and severely limit our ability to predict or explain trends in relation to changes in either fishing or the environment. We review two examples here to illustrate this point.

The first example is a modification of a simulation model developed by Frank and Brickman (2000). The objective was to determine whether or not an

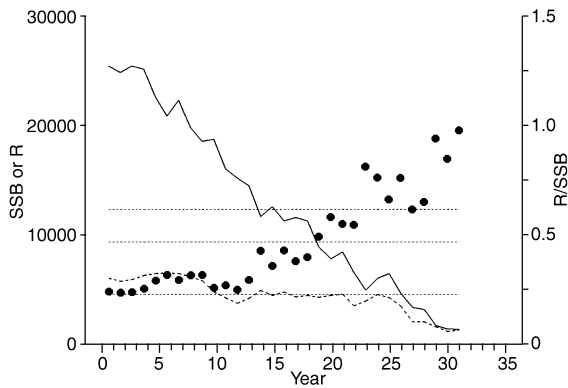


Fig. 6. Temporal trends in S (solid line), R (dashed line), and R/S (closed circles) generated from the simulation model originally developed in Frank and Brickman (2000). Horizontal dashed lines from top to bottom show the safe, minimum, and dangerous spawning stock biomass thresholds of Serebryakov (1990).

explicitly defined Allee effect in the stock and recruitment relationship at the sub-stock scale was still detectable when the data were aggregated from several sub-stocks at the management unit scale. In this model each sub-stock has its own Ricker S – R relationship exhibiting an Allee effect, and a random initial S . At each time-step, S is decremented by a constant catch (Hillborn and Walters (1992) so-called “one-way-trip”), and incremented by a recruitment equal to $1 \pm$ random fraction of the $R(S)$ of the particular sub-stock (see Frank and Brickman, 2000 for more details). The model keeps track of aggregated quantities, i.e. at the management unit scale, and the evolution of individual sub-stocks. Some may consider constant catch to be an unreasonable assumption, but numerous examples support it (e.g. see Daan, 1997).

As an illustration, we ran the model for 31 years with 6 sub-stocks. This was intended to bear a mild resemblance to the Northern cod scenario previously described. The simulation results are illustrated as a time trajectory of S , R , and R/S at the management unit scale (Fig. 6). S declined monotonically and R exhibited a cascading decline consistent with the expectations of Sinclair et al. (1985) for a management unit subjected to erosion of sub-stock structure. Survival rates (R/S) show a strong compensatory response so that one might predict that recovery is on the way. Hidden beneath this optimistic picture is the fact that the stock structure has eroded and recruit-

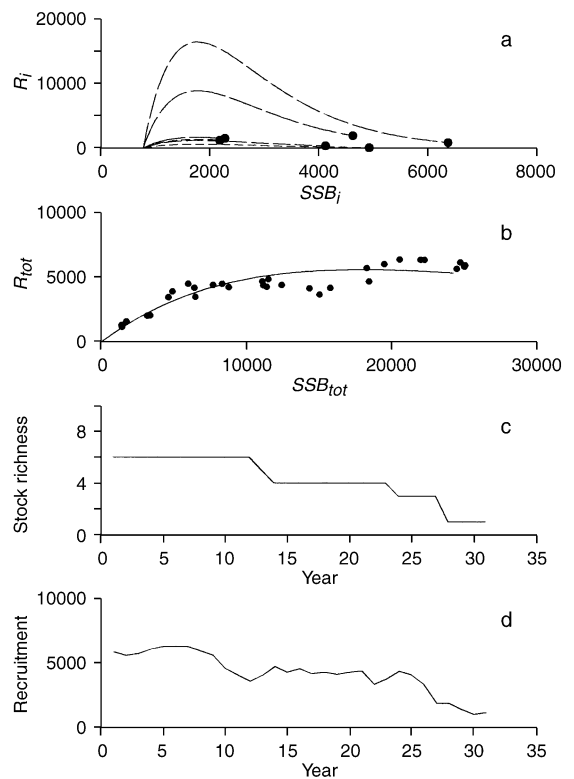


Fig. 7. (a) The assumed stock and recruitment relationship incorporating the Allee effect (positive x -intercept) for each of the six sub-stocks. The closed circles represent the randomly selected starting point for the incremental depletion of each sub-stock. (b) Recruitment versus spawning stock data at the management unit scale. The Ricker model best fit the data with the curve passing through the origin. Temporal decline in (c) the number of sub-stocks and (d) recruitment during the 31-y simulation.

ment decreased due to extinction of sub-stocks (Fig. 7c,d). However, since there is only 1 sub-stock remaining after 31 years, recovery would require knowledge of the metapopulation behaviour of the management unit. The Serebryakov (1990) minimum and dangerous SSB thresholds were exceeded in year 19 and 27 (Fig. 6) respectively, well into the process of sub-stock erosion. Furthermore, despite the fact that each sub-stock S – R relationship exhibits an Allee effect (Fig. 7a), the aggregate S – R relationship is best fit by a zero intercept Ricker curve (Fig. 7b). We note that since the model has random components, the figures represent possible outcomes. However, analysis of model results showed that over 90% of the aggregate S – R relationships were better fit by a

zero-intercept Ricker curve than one with an Allee effect, and the R/S-S relationships were similarly robust. The appearance of a cascading R-effect, as predicted by Sinclair et al. (1985), was surprisingly, rarely observed. In summary, our simulation modelling has provided some insights into why collapsed stocks have failed to recover and points to the possibility that Allee effects may be more common than conventional fisheries data suggest.

The second example, also based on a simulation model, was developed by Daan (1991) to evaluate the effect of combining data from two, differentially exploited sub-stocks into a single analytical assessment or VPA (virtual population assessment). The principal result was that even though the exploitation patterns imposed upon the individual sub-stocks were flat-topped, the combined assessment yielded a dome-shaped exploitation curve. This bias may cause significant underestimates of fishing effort due to associated change in the apparent catchability of the older age groups and render highly inaccurate trends in both fishing mortality and spawning stock biomass. It appears that for mixed populations there is not a direct relationship between the overall fish mortality and total fishing effort, if the pattern of fishing effort is different for each sub-stock. In the extreme case of over-fishing one of the sub-stocks to the point of extinction, the combined assessment would indicate that fishing mortality was gradually declining. Such a bias in VPA when the unit stock assessed consists of sub-stocks, may easily lead to inappropriate management advice. The author did not offer a solution to correcting the bias other than to assess the different components individually, which was considered not to be a practical solution.

6. Fisheries management and conservation of intra-specific diversity

A management approach with the objective of preventing the elimination of sub-stocks will require a re-definition of the space/time scales of the management unit. The most appropriate scale to meet this objective is at the level of the sub-stock at a time when there is little or no mixing among sub-stocks. Fishing close to the time of spawning when the sub-stocks are segregated is one approach to dealing with

this problem. This implies a significant reduction of fishing effort on the mixed phases of the life history. It will also require an exploitation pattern that is evenly distributed among the individual sub-stocks, e.g. distributing fishing effort in a manner that is proportional to the productivity of the individual sub-stocks. Sinclair et al. (1985) suggested that this type of management plan was required for Atlantic herring in the northwest Atlantic and recently, such a plan — an “in-season management approach” was instituted in the southwest Nova Scotia herring fishery (Stephenson et al., 1999). The plan involves pre-season surveys of each sub-stock to assess their size and state, restriction of fishing to a portion (less than 20%) of the estimated sub-stock biomass, and a potential for further restrictions in real time depending on observations from the fishery. Since the institution of the new management system, the herring stock complex has steadily improved. However, other factors have changed as well, such as a major reduction in a potential predator — cod, and it is known from other geographic areas that cod and herring exhibit reciprocal oscillations in abundance (Swain and Sinclair, 2000). It is probably too early to draw conclusions about the impact of this management system. Because such a system demands a high level of involvement from all participants in the fishery management process (Stephenson et al., 1999) a careful evaluation is warranted.

Another approach to managing for maintenance of intra-specific diversity is to establish no-take zones (or closed areas) to enable sub-stocks to escape fishing. The expectations of areas protected from fishing are numerous and have been discussed in the literature dealing with marine reserves or marine protected areas. At a workshop on the design and monitoring of marine reserves, Pitcher (1997) listed several benefits that can accrue from areas protected from fishing. These included: restricted fishing mortality, protection against stock collapse, enhancement of spawning biomass, recruitment, and survival of older fish, increase in fisheries catches in contiguous areas, insurance against over-fishing, buffering ineffective control over fishing effort, providing a buffer against uncertainty associated with stock biomass estimates, and so on. Unfortunately, most of these benefits have been modelled rather than directly demonstrated with the exception of some examples from tropical reef systems (Rowley, 1995).

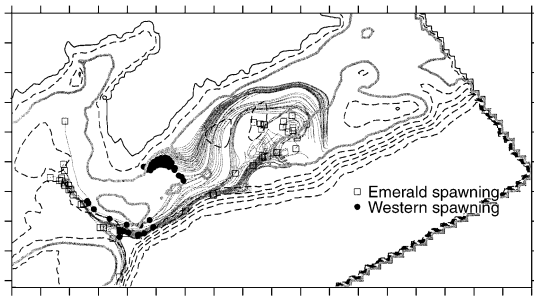


Fig. 8. Simulated trajectories of particles (haddock eggs and larvae) in 1983, based on ocean circulation modelling. Particles were released on Western and Emerald bank during springtime in the top 20 m of the water column. The final particle positions, after a 60 d period, are depicted as symbols. The displacement of particles was on the order of 200–300 km.

Currently, there are no clear demonstrations of the benefits for fisheries of areas protected from fishing in marine temperate ecosystems. This is not for lack of trying — closed areas, designed to protect juveniles or the adults of commercially important groundfish stocks, have been implemented in several management units during the past decade (Frank et al., 2000). Evaluation of the effectiveness of these closed areas as a tool for achieving fishery management objectives has revealed some common themes. The biomass of the target species generally increased inside the protected areas following their establishment, however increases in stock biomass at the scale of the management unit have not been observed. This can be explained by the fact that intense fisheries operating in surrounding areas frequently offset the benefits achieved within the closed areas (Pastoors et al., 2000). Establishing a closed area under a TAC regulation has led to effort displacement which can be detrimental to sub-stocks (Fogarty and Murawski 1998). In a modelling study, Parrish (1999) has shown that a by-product associated with the establishment of large marine reserves is a considerable increase in fishing mortality rates in open areas and that reserves may result in decreases in recruitment depending upon the source of density-dependence in the S–R relationship. Area closures in combination with effort controls are needed to achieve overall reductions in fishing mortality. Closed areas will not be the savior of fishery management problems, particularly the protection of individual sub-stocks, and one should not lose sight of the fact that over-all reduction in fishing effort is required for most stocks.

Recently, through bio-physical modelling, we have been evaluating the “spill-over” potential of a closed area designed to protect juvenile haddock on the Scotian Shelf. On average, haddock eggs, larvae and early juvenile stages remain in the vicinity of the offshore banks where they are spawned. However, in some years (particularly 1983 — see Frank, 1992) it has been observed that juvenile haddock drift downstream and contribute to the recruitment in an adjacent stock. Our simulation modelling studies have captured this dynamic pattern revealing that particles released (or spawned) on the offshore banks of the central Scotian Shelf (Western and Emerald) during springtime were displaced downstream to reside within the domain of the adjacent stock (Fig. 8). The spill-over effect may indeed be one of the principal benefits of areas protected from fishing. Future modelling efforts are underway to evaluate inter-annual variability in immigration and emigration rates that appear to couple these adjacent stocks.

7. Conclusions

One of the most pressing biodiversity issues in marine fisheries is the protection of sub-stocks. Most stocks appear to have a complex population structure and will require a reduction in the space/time scales of fisheries management in order to be sustainable in the future. Whether or not this new conservation strategy will result in the re-establishment of a complex population structure in collapsed stocks is not known. If Allee effects are indeed operative and not uncommon in marine fishes, then immigration from adjacent sub-stocks will be required to reach or exceed the threshold population levels needed for successful reproduction and the recovery of extant sub-stocks. The dynamics of fish populations artificially reduced to low levels is poorly known and behavioural changes in those species, normally adapted to life at higher densities, are likely to be extreme. Logistics may prevent the execution of field studies investigating such phenomena but the possibilities for experimental work on extinction dynamics may be numerous (e.g. see Belovsky et al., 1999).

Defining threshold population levels is an important requirement of fisheries management. However, target and limit reference points based on

conventional fisheries data (i.e. aggregated at the scale of the management unit) are likely to be non-conservative. The Serebryakov (1990) method has some appealing features that if applied at the sub-stock scale could provide some meaningful reference points. Violation of the unit stock assumption is widespread and has limited our ability to predict or explain population trends in relation to changes in either fishing or the environment.

Some have argued that biodiversity can be maintained or enhanced by establishing area closures or “no-take” zones. Unfortunately, area closures and MPAs do not represent viable, stand alone alternatives to fisheries management but require blending into existing management measures including overall reductions in fishing effort. Threats to biodiversity, in particular intra-specific diversity, may actually be heightened when no reductions in fishing effort accompany area closures.

It would be highly beneficial for both fisheries scientists and conservation biologists, who appear to be following somewhat parallel paths, to initiate an exchange of ideas and experiences associated with resource evaluation and management. Fisheries scientists have a vast array of quantitative tools and approaches to resource evaluation and management that would be of direct interest to conservation biologists. On the other hand, conservation biologists appear to want to incorporate a much broader base of information in order to evaluate the contemporary and future status of populations, including incorporation of stochastic variation, genetics, demography and ecology. Such information is rarely contained in conventional fish stock assessments, but there are some new approaches on the horizon (e.g. the traffic light approach of Caddy, 1999b) that will make significant steps towards correcting this deficiency.

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