A conceptual framework for enhancing and studying recruitment of marine fish stocks

A. FOLKVORD, G. BLOM, O. DRAGESUND, A. JOHANNESSEN
Department of Fisheries and Marine Biology, University of Bergen, Bergen, Norway
O. NAKKEN Institute of Marine Research, Bergen, Norway
G. NÆVDAL Department of Fisheries and Marine Biology, University of Bergen, Bergen, Norway

Abstract. The possibility of enhancing and studying recruitment of commercially important marine fish stocks is discussed in general, and for North-east Atlantic cod stocks, Gadus morhua L., in particular. Current knowledge concerning the relative importance of different physical and biological factors influencing survival of early stages is addressed in relation to cost-benefit of release programmes.

The cost of producing large juveniles is relatively high compared with the expected yield per recruit. Because large juveniles also eventually become too expensive to release, emphasis should be put into releasing the offspring as early as possible. Special attention is given to evaluation of the optimal time for survival of larvae and juveniles and thus the possibility to enhance recruitment by releasing the offspring when environmental factors are favourable.

The prey energy available for larval and juvenile fish varies during ontogeny. The period at the onset of exogenous feeding and the early juvenile period are hypothesized to be critical windows in relation to recruitment. Experimental designs in closed and open enclosures for further investigations of the importance of food availability, predation and cannibalism are outlined, with use of genetic and otolith marking for identification of different cohorts.

Introduction

Fish stocks will through evolutionary processes be adapted to availability, size spectrum and abundance of the prey organisms in the region of stock distribution. Environmental conditions, both abiotic and biotic, will influence the distribution and development of larval and juvenile stages.

For many stocks, to maintain their general distribution pattern, the adults have to carry out compensatory movements in the direction opposite to the larval drift before, and in connection with, spawning (Harden-Jones 1968). Thus the spawning time and area, and prevailing ocean currents, determine when and where larvae and juveniles will develop.

The adaptation of fish stocks to their most common prey organisms can be perturbed by anthropogenic effects. Fishing will alter the age and population structure of the spawning stock, and thus may influence both the spawning period and area, i.e. larval development in time and space (Pedersen 1984).

Correspondence: Dr A. Folkvord, Department of Fisheries and Marine Biology, University of Bergen, High Technology Centre, N-5020 Bergen, Norway.
In this paper, a conceptual framework is presented for studying the possibility of enhancing and stabilizing recruitment of fish stocks. The background for this concept is the assumption (hypothesis) that the stock area carrying capacity is large enough to sustain a higher average level of recruitment than the stock has experienced during the last decades. In particular we will focus on the timing of prey availability in relation to larval growth and development, in addition to the regional abundance of suitable larval and juvenile prey. Some important gaps in our knowledge to utilize this potential are discussed with the aim to stabilize recruitment. The argumentation is meant to be general although the North-east Atlantic cod, *Gadus morhua* L., stocks are particularly in mind. In this context the principal prey is the calanoid copepod *Calanus finmarchicus*. Cod larger than 12 mm are defined as juveniles, and at this stage the larval finfold has been replaced by dorsal and anal fins (Pedersen & Falk-Petersen 1992).

The enhancement potential is believed to be linked to the possibility of compensating for mismatch between larval or juvenile fish and their prey. An experimental design is proposed to test the importance of two critical periods or windows through which the larvae and juveniles will have to pass during development: the first feeding period and the early juvenile period. The copepod *C. finmarchicus* is hypothesized to be the critical prey, with nauplii important at first feeding and copepodite stages in the later period.

**Synthesis**

*Cost—benefit of production of cod juveniles*

The costs involved in rearing cod larvae and juveniles in closed and controlled systems increase rapidly with juvenile size/age. Larval demand for food and space may generate extensive cannibalism and hence high mortality unless measures like sufficient food supply and sorting by size are implemented (Øiestad, Pedersen, Folkvord, Bjordal & Kvenseth 1987; Folkvord 1991). The money and manpower needed to secure sufficient survival beyond metamorphosis may reach a level at which the juveniles become too expensive to be released.

Releasing cod juveniles late in the 0-group stage or in the 1-group stage will most likely reduce their mortality (Svåsand & Kristiansen 1990). The question remains whether it would be more profitable to keep the juveniles one more year in captivity until they approach a marketable size of 2 kg (Braaten 1984; own unpublished data).

When the cod juveniles are reared beyond 20 mm in enclosures, they will require addition of formulated feed (Blom, Otterå, Svåsand, Kristiansen & Serigstad 1991). In a sea-ranching context it is possible that learning of young cod to accept formulated feed can have negative effects after release. It has been shown that wild and reared animals may differ in feeding behaviour and predator naivety (Blaxter 1975; Nordeide & Salvanes 1991). The overall effect on subsequent survival after release is, however, unclear.

Svåsand & Kristiansen (1990) have calculated mortalities of released 0-group cod. These mortalities generate yield per recruit (per released individual) figures of 0.1–0.2 kg. Although these figures could be improved considerably by changing the exploitation pattern, it is highly questionable whether rearing beyond metamorphosis before releasing will meet any cost—benefit requirements. With the purpose of enhancing recruitment of fish stocks, i.e. enhancing and stabilizing fisheries, effort should be put into evaluating the
possibility of liberating spawning products at an earlier stage than hitherto (Tsukamoto, Kuwada, Hirokawa, Oya, Sekiya, Fujimoto & Imaizumi 1989).

Aspects of prey size and suitability

The mouth size of fish larvae generally increases with larval size, and it physically restricts the range of prey sizes available to the larvae (Shirota 1970; Hunter & Kimbrell 1980; Kane 1984). At the spawning grounds in Lofoten, the most important food item for cod during the first weeks of exogenous feeding is naupliar stages of C. finmarchicus (Ellertsen, Fossum, Solemdal & Tilseth 1984). The width of the nauplii varies between 0.18 and 0.33 mm (Wiborg 1948a). The later copepodite stages of C. finmarchicus are not readily ingested by cod larvae less than 10–15 mm (Kane 1984; Fig. 1), and adults are not proportionally consumed before the cod exceed 20 mm (Wiborg 1948a; Sysoeva & Degtereva 1964; Otterå & Folkvord 1993). Thus there is an optimal range of prey sizes, and the range and mean increase during ontogeny. Typically the average prey width is around one-third to one-half of the mouth diameter (Shirota 1970; Hunter & Kimbrell 1980). The growth of C. finmarchicus is parallel to the growth of the cod larvae, and thus the number of nauplii produced within a given time period will also influence the food availability during late larval and early juvenile stages (Jones & Hall 1974).

Aspects of prey abundance

The amount of prey available for cod larvae is defined by the biomass spectra in their habitat.* Several plankton investigations along the Norwegian coast and in adjacent

![Figure 1](image-url)  
* Biomass spectrum is biomass density as an allometric function of organism size plotted on a log–log scale (Boudreau & Dickie 1992)
waters have shown the dominance of the copepod *C. finmarchicus* (e.g. Wiborg 1948b, 1976; Lie 1965, 1968; Economou 1987; Tande 1992). Up to 90% of the copepods in numbers, corresponding to over 90% of the plankton volume, consisted of various stages of *C. finmarchicus* (Wiborg 1954). In northern waters, *C. finmarchicus* typically has one main spawning period in spring, and in some regions a smaller and less important spawning during early fall depending on temperature (Fig. 2; Østvedt 1955; Lie 1965, 1968).

The importance of *C. finmarchicus* in the diet of larval and juvenile cod has been confirmed in several studies of stomach contents (Wiborg 1948b; Sysoeva & Degtereva 1964; Ellertsen *et al.* 1984; Thorisson 1989; Helle, in press). The naupliar stages constitute the main prey item during the early larval stage, and the later copepodite stages become increasingly important later on (Jones & Hall 1974).

The availability of suitable prey for fish larvae during onset of exogenous feeding has been hypothesized to represent a critical window for recruitment (Hjort 1914; Dragesund 1970; Cushing 1990). A temperature-related mechanism of match—mismatch of cod larvae and *C. finmarchicus* nauplii has been suggested to explain the variable recruitment of the North-east Arctic cod stock (Ellertsen, Fossum, Solemdal & Sundby 1.989). The time of maximum occurrence of *C. finmarchicus* CI stage has been observed to vary with 1-5 months between years, and this difference in temporal abundance is expected to propagate to later stages. In the North Sea a 1-month delay of peak occurrence of *C. finmarchicus* has been demonstrated (Cushing 1984, Fig. 3). The increase in gadoid biomass in the area in the period 1962–1978 has been suggested to be a result of increased prey availability to the larval and juvenile fish (Cushing 1984).

There is a substantial regional variability in the abundance of *C. finmarchicus* along the Norwegian coast and adjacent waters (Lie 1965; Wiborg 1976; Brander 1992). Generally
the zooplankton biomass around the Lofoten Archipelago, the main spawning ground of North-east Arctic cod, is higher than in other areas along the coast (Lie 1965; Wiborg 1978; Fig. 4). However, the variation between years within each station is considerable.

**Effects of prey availability on fish growth and recruitment**

Starvation in fishes is presumably most important during the onset of exogenous feeding (Hjort 1914; Hewitt, Theilacker & Lo 1985). Starving juveniles are not commonly encountered in the field (Houde 1987), and 20 mm cod juveniles survive more than a week of food deprivation (Folkvord 1991). This has led to the emphasis of predation as an important regulatory mechanism (Bailey & Houde 1989). Reduced individual growth rate will, however, result in a longer stage duration in a vulnerable size range, and thereby result in reduced survival through predation (Shepherd & Cushing 1980).

Growth will be reduced if fish do not overlap with prey in time and space. The condition factor of larval cod has been demonstrated to correlate with zooplankton abundance (Koslow, Brault, Dugas, Fournier & Hughes 1985). Recent growth as determined by otolith microstructure or RNA/DNA ratios has been related to zooplankton biomass in the suitable size range (Buckley & Lough 1987; Suthers, Frank & Campana 1989). The observation that larval and juvenile fish co-occur with their principal prey may be a manifestation of higher survival in areas supporting higher growth rates (Sysoeva & Degtereva 1964; Fortier & Harris 1989; Helle, in press).

The availability of prey and the growth in the early juvenile stage have been hypothesized to regulate recruitment of several marine fish stocks (Anderson 1988; Bollens, Frost, Schwaninger, Davies, Way & Landsteiner 1992). This can partly be explained by the marked increase in food demand of individual fish through ontogeny (Fig. 5; Table 1; Blom et al. 1991). Due to higher growth rates and temperatures encountered during the early juvenile stage, a newly metamorphosed cod requires nearly 50–100 times more energy than a first feeding larva. The growth rate is also higher than the mortality rate.
Figure 4. Spatial abundance distribution of zooplankton (mainly C. finmarchicus) per m² from 50–0 m (100–0 m at Station M) along the Norwegian coast (modified from Wiborg 1978).

during the juvenile stage (Sundby, Bjørke, Soldal & Olsen 1989) resulting in an increase in fish biomass at this stage. Ten 45-day-old larvae will have the same consumption (in J) as one 20-day-older juvenile, whereas ten 65-day-old cod juveniles will have the same consumption as one 70-day-older juvenile (Fig. 5). The food level can limit the final recruitment (Cushing 1983), and the time after metamorphosis may be a critical period or window for survival due to the rapid increase in food demand. We suggest that this window is determined by the availability of late copepodite stages and adults of C. finmarchicus to early cod juveniles.

The possibility of recruitment enhancement and control

The ultimate goal of a sea-ranching programme is to secure a higher and more stable recruitment of fish (Svåsand & Kristiansen 1990). Implicit is the assumption that in certain
Figure 5. Consumption of 1 cod larva and 10 cod larvae based on model from Blom et al. (1991) and using growth values from Table 1 (solid line for one larva, broken line for 10 larvae). The lengths of the horizontal arrows represent age differences where these two groups will have the same daily consumption.

Table 1. Dry weight and daily consumption of individual North-east Arctic cod*. Corresponding numbers of Calanus finmarchicus equivalents are indicated

<table>
<thead>
<tr>
<th>Age in days</th>
<th>Dry weight (mg)</th>
<th>Consumption (J)</th>
<th>Weight specific consumption</th>
<th>Nauplii equivalents (3.2 µg)</th>
<th>CI–CII equivalents (14.4 µg)</th>
<th>CI–IV equivalents (71.2 µg)</th>
<th>CV–Adult equivalents (230.6 µg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>0.05</td>
<td>0.222</td>
<td>4.44</td>
<td>3.3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>0.08</td>
<td>0.354</td>
<td>4.54</td>
<td>5.1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>0.19</td>
<td>0.906</td>
<td>4.72</td>
<td>13.3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>30</td>
<td>0.47</td>
<td>2.320</td>
<td>4.94</td>
<td>33.6</td>
<td>7.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>40</td>
<td>1.15</td>
<td>5.951</td>
<td>5.17</td>
<td>86.2</td>
<td>18.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>50</td>
<td>3.22</td>
<td>32.237</td>
<td>9.99</td>
<td>100.0</td>
<td>20.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>60</td>
<td>8.22</td>
<td>79.611</td>
<td>9.68</td>
<td></td>
<td>50.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>70</td>
<td>39.85</td>
<td>122.835</td>
<td>3.08</td>
<td></td>
<td>77.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>80</td>
<td>71.74</td>
<td>161.908</td>
<td>2.27</td>
<td></td>
<td>101.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>90</td>
<td>102.44</td>
<td>223.256</td>
<td>2.18</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>100</td>
<td>146.83</td>
<td>307.898</td>
<td>2.10</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>110</td>
<td>210.46</td>
<td>425.180</td>
<td>2.02</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>120</td>
<td>310.66</td>
<td>587.655</td>
<td>1.89</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>130</td>
<td>432.39</td>
<td>816.170</td>
<td>1.89</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>135</td>
<td>517.67</td>
<td>963.080</td>
<td>1.86</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Growth in length of cod from Sundby et al. (1989) and corresponding estimated weights from Thorisson (1989). Consumption and copepod equivalents based on a model from Blom et al. (1991). Environmental temperatures set to 6, 8 and 6.5°C during periods 5–45, 45–75 and 75–135 days respectively (Institute of Marine Research, Bergen, unpublished data).
periods and/or areas there are prey organisms available which are not being fully utilized because of regional and/or temporal mismatch between fish and prey. We have documented temporal and regional variations in the availability of the principal prey item, *C. finmarchicus*. The question still remains if we are able to use this information to obtain acceptable results from our enhancement efforts. A sea-ranching programme ensuring a better representation of fish in time and space, i.e. ensuring match, may thus counteract the effects of such a 'natural' mismatch. This can be achieved in two ways, (a) by artificially extending the spawning season (the period of larval release), or (b) by specifically releasing larvae at a time and place where they will match the prey availability (Fig. 6).

Density-dependent processes may limit the potential of a sea-ranching programme (Peterman 1991). Cannibalism has been suggested to be a stabilizing mechanism preventing excessive mortality due to temporary food limitation (Nellen 1986; Folkvord 1993). Density-independent mortality mechanisms, such as advective losses of larvae to unfavourable feeding areas, are unaffected by the added contribution of larvae or juveniles in a sea-ranching programme. Density-dependent regulation can take place in the early juvenile stage (Houde 1987; Dwyer, Bailey & Livingston 1987; Svåsand & Kristiansen 1990), and in later juvenile stages, 1–III group fish, if the feeding conditions are especially unfavourable (Mehl 1988; Nordeide 1993). If these mechanisms are dominant controlling factors determining recruitment, the prospects of enhancement programmes are dubious (Jones 1973; Ulltang 1984). However, Sundby *et al.* (1989) found a relatively good correlation between abundance indices at the early juvenile stage and recruits as III-group in North-east Arctic cod.

Large-scale experiments in enclosures under semi-natural conditions can be carried out to study the factors which regulate year-class strength in marine fishes (Oiestad 1990). Below we have defined two periods that are hypothesized to represent critical periods or windows in terms of recruitment determination and we have described experimental designs for testing these hypotheses.

**Figure 6.** Match—mismatch of larvae and their prey. Two alternative release periods of enhancement are indicated (modified from Cushing 1990).
Proposed investigations

Window 1. First feeding period

Field and enclosure experiments can be conducted to study the optimal time for first feeding of larvae relative to plankton availability and composition. It is supposed that a semi-enclosed small fjord or pond (hereafter called the open system), and replicate closed pens of 500—1000 cubic metres (hereafter called the closed systems) are available. Over the last decade, ponds have been used at several locations along the Norwegian coast to produce juvenile cod (e.g. Øiestad, Kvenseth & Folkvord 1985; Pedersen, Eliassen, Eilertsen, Tande & Olsen 1989; Blom et al. 1991). Parallel experiments should be carried out both in open and in closed systems. Previous experiments with larval cod in pens have shown good replicability between parallels with regards to larval growth and survival (Otters 1993). The closed systems are located within the open system, and the physical and biological environment are kept identical as far as possible within the two systems.

It is supposed that natural spawning of cod is taking place in the open system. In addition large numbers of cod eggs and larvae can easily be obtained from captive broodstocks (Huse & Jensen 1983; Solemdal, Dahl, Danielssen & Moksness 1984). The open system will simulate the area to be enhanced, with its own population, whereas the closed systems will represent specific control groups.

Newly hatched larvae are liberated repeatedly and simultaneously in the two systems. Additional information can be gained by parallel experiments in several locations along the coast. It is important that all larvae which are liberated are in the same stage of development. If necessary, spawning time of the parent fish must be regulated by manipulation of light regimes (Carrillo, Bromage, Zanuy, Serrano & Prat 1989). In the closed system, separate new pens are used each time to make the different liberations independent. To distinguish between larvae of the different batches and between naturally occurring and liberated larvae in the open system, genetic marking and/or chemical marking can be used (Anon. 1991; Svåsand, Jørstad, Blom & Kristiansen 1991; Blom, Nordeide, Svåsand & Borge 1994; Blom, Svåsand, Jørstad, Otterå, Paulsen & Holm in press). A genetic mark (homozygote GPI-1*30/30) is available, and for long-term experiments new ones may be developed (Jørstad, Skaala & Dahle 1991).

A frequent and intense sampling programme has to be carried out in both systems before, during and after the liberation of larvae. Zooplankton should be added to the closed system to compensate for density-dependent grazing and the lack of larval diffusion and advection.

Survival, growth and dispersal of the different batches of larvae in the open system have to be followed from hatching to beyond metamorphosis, and the plankton communities have to be monitored with respects to biomass, species composition and size (stage) composition. Providing that the experiments are conducted according to the outlined plans, the results are expected to give considerable new information about the match—mismatch theory, and also about the importance of predation and cannibalism (differences between the open and the closed system) for larval survival.
Window 2. Early juvenile period

The production and biomass of suitable prey in the early juvenile stage is hypothesized to impose a limit on the production of juvenile fish. Modelling studies also indicate that density-dependent recruitment mechanisms may be important in the juvenile stage (Shepherd & Cushing 1980; Houde 1987; Blom et al. 1991; Bradford 1992). In the case of cod, the data suggest *C. finmarchicus* to be the key prey species influencing recruitment. The rationale for such a hypothesis is partly based on the observation that in some years, large year classes of several species are produced. This suggests that large-scale climatic or advective events are directly or indirectly involved in the formation of year-class strength (Sætersdal & Loeng 1987). Such events may influence plankton production and distribution, and subsequently fish growth and survival (Nordeide 1993).

As a first step, one should investigate existing time series from field and enclosure studies with respect to prey abundance, fish growth and survival. Trends in prey abundance should, if possible, be coupled with climatological data to find controlling factors (e.g. Cushing 1984; Brander 1992). In the case where appropriate data are not available, we recommend the initiation of a quantitative field sampling programme of zooplankton and juveniles. Possible abiotic controlling factors should also be measured. A research programme, ‘Cod and Climate Change’, is already in operation dealing with responses of various cod stocks to changes in temperature and climate (Anon. 1991). This programme specifically deals with stock-specific growth and survival potential under optimal feeding conditions.

We recommend a test of the hypothesis that cannibalism is a controlling factor (Nellen 1986). This can be done in experimental feeding studies in enclosures where the amount of *C. finmarchicus* is sufficient to sustain maximum growth, half of maximum growth, minimum growth (Beyer & Laurence 1981), and maintenance growth (no net growth). The experiments related to window 2 should be an extension of the experiments related to window 1 because the timing of the zooplankton production is expected to be of importance into the juvenile stage.

Otolith microstructure can reveal differences between individual growth rate and population growth rate, and thereby give estimates of mortality (Houde 1987). The use of genetically marked fish (see above) can also give added information on size-dependent mortality aspects. The experiments related to the second window could be terminated when *C. finmarchicus* is no longer the dominant food item. This would correspond to a juvenile size of around 4–5 cm when the cod shift towards larger prey, such as krill (Wiborg 1960; Sysoeva & Degtereva 1964).

Concluding remarks

A mismatch between fish larvae and larval prey can result in a lower recruitment due to suboptimal feeding conditions. A sea-ranching programme can possibly compensate for this mismatch by releasing offspring at a time better in accordance with the natural plankton production. We therefore recommend the initiation of large-scale enclosure experiments specifically dealing with abundance and size spectrum of prey related to growth and survival of fish larvae. These experiments will have to be viewed in light of the ongoing research programme on ‘Cod and Climate Change’, and a new research programme
Recruitment of marine fish stocks

in progress in Norway, ‘Mare Cognitum’. An important aspect in the latter programme is the coupling between climate, physical oceanography and the dynamics of *C. finmarchicus* in the Norwegian Sea. An understanding of these factors together with knowledge of the temperature-dependent growth and survival potential of cod is closely linked to the proposed experiments. Information from all three areas is necessary to understand observed recruitment variability in cod and to possibly stabilize it through enhancement.

**Acknowledgment**

The helpful suggestions and corrections of Clelia Booman are greatly appreciated.

**References**


Recruitment of marine fish stocks


Thorsson K. (1989) The food of larvae and pelagic juveniles of cod (*Gadus morhua L.*) in the coastal waters of


