

Integration of Captive and Wild Studies to Estimate Egg and Larval Production of Fish Stocks

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Abstract

Experimental work on the reproduction of captive marine fish species provides the opportunity to improve our knowledge of the factors and mechanisms regulating reproduction of fish populations in natural environments. The integration of captive and wild studies can potentially be used to predict changes in the reproductive characteristics of fish populations in response to variations in specific environmental conditions in the wild. This dual approach can also be used to develop predictive models incorporating biological and environmental factors. However, differences in the acclimation to captivity, reproductive strategy, reproductive behaviour and susceptibility to stress may limit the extrapolation of laboratory work on different captive fish species to situations in the wild. For each species, some form of validation will be necessary to determine which of the different reproductive characteristics determined experimentally can be applied to wild fish. Wild fish should preferably be kept in captivity for limited periods of time prior to laboratory experiments and holding conditions should mimic environmental conditions as closely as possible. Natural food should be preferred to formulated feeds and the quantity of food should be adjusted to obtain growth, maturation and reproductive effort in the range observed for wild fish. Repeatability of experimental results should be evaluated by comparing the results of more than one experiment with the same experimental protocol and/or by using the same protocol in different laboratories.

Key words: cod, condition factor, eggs, fecundity, fertilization, fish, flatfish, marine, reproduction, tank experiments, wild stock, captive studies.

Introduction

Experiments with captive fish cannot reproduce conditions observed in the wild, but they can nevertheless provide tools to estimate and understand mechanisms causing variability in egg and larval production in wild populations. Design of experimental studies as well as constraints associated with species under study will determine our capacity to use the results of these captive fish studies to estimate the reproductive potential of wild stocks.

Methods used to study the reproduction of captive marine fishes can be very different. Thus, the possible applications of the results to wild fish populations will differ depending on species and methodology of study. Some form of species-related validation will be necessary in order to determine which of the different experimentally-determined reproductive parameters can be applied to wild fish.

This contribution presents species-specific approaches used to study the reproduction of marine fish in the laboratory. The reproductive strategy, husbandry conditions, manipulations of the fish, reproductive characteristics measured and the advantages and limitations associated with each approach are examined. This information is used to evaluate the potential applications of laboratory experiments to estimate the reproductive characteristics and reproductive potential of wild fish stocks.

Species suitability to captivity and laboratory studies

Most marine fish species used for laboratory experiments are determinate spawners (Murua and Saborido-Rey, 2003). Both total and batch spawners have been studied. However, studies on batch spawners require more elaborate logistics since each female has to be followed individually and very often for long periods of time. In these situations, experiments will generally be completed on a limited number

of fish. For example, studies on the egg production of Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), American plaice (*Hippoglossoides platessoides*) and yellowtail flounder (*Pleuronectes ferrugineus*) were typically conducted using 10 to 20 females per spawning season (Hislop *et al.*, 1978; Kjesbu, 1989; Chambers and Waiwood, 1996; Kjesbu *et al.*, 1996; Manning and Crim, 1998; Trippel, 1998; Nagler *et al.*, 1999; Lambert and Dutil, 2000).

Factors to consider for laboratory experiments on reproduction include the method of capture and the behaviour of the selected fish species in captivity. The capture and transport of wild fish for laboratory experiments always induces some stress and mortality. Common methods of capture for marine fish include trawl, seine, hook and line, trap and SCUBA diving. These methods can induce injuries to the skin, mouth and jaws that can eventually lead to osmotic problems and infections. The depth of capture for physoclistic species (e.g. cod) can also induce injuries due to the expansion of gases as fish are brought to the surface. Rupture of the swimbladder, gas embolism and exophthalmia are some of the injuries that can result from depressurization (Bruesewitz *et al.*, 1993). Fish must be captured early enough to let them adapt to captivity before commencing experiments. Acclimation periods between 1 and 4 months are often observed for wild fish brought to the laboratory (Dutil *et al.*, 1992; Ma *et al.*, 1998). However, fish have been caught several (6–12) months and even years before being used in some reproductive experiments (Manning and Crim, 1998; Trippel, 1998; Trippel *et al.*, 1998; Morgan *et al.*, 1999; Nagler *et al.*, 1999; Lambert and Dutil, 2000). These longer acclimation periods prevent possible disruption of the maturation cycle due to the stress of capture and allow the manipulation of experimental conditions before the onset of maturation.

Many species adapt quickly and appear to behave normally in captivity. For example, wild cod captured with long lines or bottom trawl and brought to captivity in good condition quickly resume feeding, are resistant to disease and have good survival rates. Other species, such as winter flounder (*Pseudopleuronectes americanus*), can be less suited to captive conditions. Winter flounder broodstock can experience major losses associated with handling stress or due to fin or tail-rot diseases (Hoornbeek *et al.*, 1982; Burton and Idler, 1987; Harmin and Crim, 1992), although such problems have not been mentioned elsewhere (Litvak, 1999). Finally, some species are less suited to laboratory experiments due to high mortality rates at capture. For

example, spawner mortality of wild sole (*Solea solea*) can be high during the first month of captivity (Devauchelle *et al.*, 1987). Losses of Atlantic herring (*Clupea harengus*) during the first month of captivity may range from a low of 10% (Ma *et al.*, 1998) to greater than 50% (A. Thorsen, unpubl. data) even when captured by purse seine and may be related to extensive scale loss. High sensitivity to changes in depth has prevented deepwater species such as redbfish (*Sebastes sp.*) from being maintained in good condition in captivity. However, SCUBA techniques for capturing live specimens have now been developed (Larocque, 2000).

Difficulties associated with the capture of fish and/or very long periods of acclimation to laboratory conditions can sometimes be circumvented by developing broodstocks from cultivated larvae or juvenile fish. It has been suggested that the effects of stress on broodstocks decline with each culture generation (Pankhurst and Van der Kraak, 1997). Laboratory experiments using fish hatched and raised in captivity have been conducted for some species (e.g. Kjesbu, 1989; Kjesbu *et al.*, 1991; Bromley *et al.*, 2000). However, domestication of fish may reduce the relevance of experiments designed to understand wild situations. For example, cod held under aquaculture conditions from the egg stage will usually attain much higher condition (i.e. fat reserves) and mature at a much younger age and smaller size than wild fish (Bergstad *et al.*, 1987; Svåsand *et al.*, 1996).

Other important aspects to consider for each individual species include maturation cycle, ovulation, spawning and behaviour in captivity. While most species appear capable of developing mature gonads in captivity, only a few will be able to spawn spontaneously in captivity (Crim and Wilson, 1998). Many species will have to be manually stripped of gametes or given hormonal injections to induce ovulation (Harmin and Crim, 1992; Larsson *et al.*, 1997; Crim and Wilson, 1998). In some marine fishes, including flatfishes like American plaice and winter flounder (Harmin and Crim, 1992; Nagler *et al.*, 1999) the absence of appropriate environmental cues or the presence of other stressors can prevent females with well-developed ovaries from ovulating. Species with more complex reproductive cycles are seldom used for laboratory experiments. Viviparous species like redbfish (*Sebastes sp.*) which have distinct periods for copulation, sperm storage, fertilization, embryogenesis and larval extrusion have not yet been used extensively in laboratory studies. Some work has been done on Pacific coast redbfish but these studies were limited to embryogenesis and larval de-

velopment most probably because these fish do not reproduce naturally in tanks (Boehlert *et al.*, 1986; Yamada and Kusakari, 1991). No signs of reproductive activity have been observed for broodstocks of Atlantic redfish (*Sebastes fasciatus*) kept in captivity for more than 2 years (Y. Lambert, unpubl. data). Nonetheless, some studies on the growth and survival of Atlantic redfish larvae have been realized, larvae near extrusion being relatively easy to obtain by stripping ripe females at sea (Laurel *et al.*, 2001).

A large repertoire of sounds and behaviours within and between sexes have been observed during the reproduction of some gadoid species (Brawn, 1961; Hawkins *et al.*, 1967; Hawkins and Rasmussen, 1978; Hutchings *et al.*, 1999; Hawkins and Amorim, 2000; Bremner *et al.*, 2002). Different behavioural acts leading to mating were associated with particular sounds in haddock (Hawkins and Amorim, 2000). A large repertoire of behavioural acts was also observed in Atlantic cod (Brawn, 1961; Hutchings *et al.*, 1999), but sound production was less versatile than in haddock (Hawkins and Rasmussen, 1978). It was suggested that sounds and the sequence of behavioural acts associated with mating played a role in synchronizing the reproductive behaviour of each gender (Hawkins and Amorim, 2000). Mating behaviour also suggests that eggs and milt are released simultaneously and in close proximity (Hawkins and Amorim, 2000). Disruption of behaviour leading to mating in captive conditions could reduce reproductive success.

Study limitations

Besides acclimation and behaviour of fish species in captivity, experimental approaches are largely dictated by the reproductive characteristics under study. To our knowledge, no study has examined the complete sequence of reproductive characteristics from potential fecundity, realized fecundity and egg and larval characteristics and viability on the same individual fish. Most studies are restricted to the evaluation of some of these reproductive characteristics due to technical limitations. The absence of techniques to measure potential fecundity without killing fish has prevented the measurement of both potential and realized fecundity on the same individual female. However, methods combining ultrasonography to determine sex and gonad size (Mattson, 1991; Karlsen and Holm, 1994; Martin-Robichaud and Rommens, 2001) and biopsy samples of ovarian tissues to count oocytes (Bromley *et al.*, 2000) could be developed. Nevertheless, information on the relationship between potential and realized fecundity has been obtained in experiments with

groups of fish. For example, Kjesbu *et al.* (1991) sampled cod that had spawned different numbers of egg batches in order to obtain measures of realized fecundity and estimates of potential fecundity. Determination of the level of atresia for different groups of fish was also used to determine the relationship between potential and realized fecundity (Kjesbu *et al.*, 1991; Ma *et al.*, 1998). There are examples of studies where many of the relationships between realized fecundity, fertilization rate, egg characteristics and survival, hatching success and larval characteristics and viability were examined for individual females (Buckley *et al.*, 1991; Marteinsdottir and Steinarsson, 1998; Nissling *et al.*, 1998; Trippel, 1998; Nagler *et al.*, 1999; Keckeis *et al.*, 2000; Ouellet *et al.*, 2001). However, studies on batch spawners are more complicated due to the amount of work and availability of experimental set-up needed to follow the different egg batches of several females.

Protocols for studying reproduction

Atlantic cod and haddock are batch spawning species that spawn on their own in captivity. They can produce between 2 and 20 egg batches during a period varying between 6 and 122 days (Hislop *et al.*, 1978; Kjesbu, 1989; Chambers and Waiwood, 1996; Trippel, 1998; Trippel *et al.*, 1998; Lambert and Dutil, 2000). Usually, male and female pairs are placed in spawning tanks and followed during the entire spawning period using collectors to retain the naturally fertilized, pelagic eggs. Volume of eggs, number of eggs spawned, proportion of eggs fertilized, egg size and egg dry weight and energy content are some of the common measures taken. Egg subsamples from different batches are used to monitor egg development, hatching success and larval size in different experimental conditions. Eggs can be incubated in groups or individually. A more complete description of methods and measurements is given by Thorsen *et al.* (2003). Some studies on eggs and larvae also used communal spawning tanks containing larger numbers of fish (Pepin *et al.*, 1997; Buckley *et al.*, 2000). However, the communal broodstock approach is restrictive when examining individual maternal effects on the size and quality of eggs (Trippel *et al.*, 1998).

Batch spawning flatfishes, such as American plaice, turbot (*Scophthalmus maximus*), yellowtail flounder and Atlantic halibut (*Hippoglossus hippoglossus*) have to be repeatedly stripped of gametes throughout the spawning season (McEvoy (Barton), 1984; Norberg *et al.*, 1991; Manning and Crim, 1998; Nagler *et al.*, 1999). These species release batches

of eggs every few days during a spawning period that can extend for 46 days. Fish are individually marked and examined for ovulation. Females with swollen abdomens are gently squeezed and then stripped if eggs are expelled. Eggs are fertilized by mixing with semen collected from mature males. Eggs of winter flounder are stripped as a single batch and are negatively buoyant and adhesive. Diatomaceous earth is currently used to prevent adhesive eggs from clumping (Buckley *et al.*, 1990; Litvak, 1999) but may damage eggs due to sharp edges on the particles (Litvak, 1999). When collecting eggs by hand stripping, care must be taken to avoid contamination by urine, feces and seawater (Dreanno *et al.*, 1998; Nagler *et al.*, 1999). Other flatfish species can potentially spawn on their own in captivity (Smith *et al.*, 1999), although reproductive output may be low (Houghton *et al.*, 1985; Devauchelle *et al.*, 1987).

Different approaches have been used to study egg and larval stages of marine fish species in captivity. In many experiments, eggs and larvae were obtained from fish that were caught in the wild and acclimated to laboratory conditions (Kjesbu *et al.*, 1991; Chambers and Waiwood, 1996; Trippel, 1998; Lambert and Dutil, 2000; Ouellet *et al.*, 2001) or from fish that were reared in the laboratory from egg to adult stage (Kjesbu *et al.*, 1996; Bromley *et al.*, 2000). Experiments on egg and larval stages have also been conducted on fish that matured in the wild. Spawning female herring have been collected at sea and quickly transported to the laboratory, where the eggs were stripped and fertilized (Laine and Rajasilta, 1999). Eggs stripped from spawning female cod captured at sea were fertilized and kept on board ship for 2–3 days before being transported to the laboratory for experiments (Martensdottir and Steinarsson, 1998). Finally, laboratory experiments on egg and larval stages have been conducted on fertilized eggs collected directly at sea with plankton samplers (Riveiro *et al.*, 2000). Methods and measures to determine the quantity and quality of eggs and larvae produced by captive marine fish are reviewed by Thorsen *et al.* (2003).

Comparison of field and laboratory measurements

Potential fecundity can be accurately measured in both field and captive conditions (Bagenal, 1978; Thorsen and Kjesbu, 2001; Murua *et al.*, 2003). Comparisons of the results obtained in both situations can then be used to validate the use of laboratory experiments to improve and understand the variability of fecundity estimates in the wild. Nevertheless, some precautions must be taken before extrapolating labora-

tory results to field situations. Husbandry conditions may produce results that are not in the range observed in wild fish. For example, captive cod in the study of Kjesbu *et al.* (1991) had higher condition factors and potential fecundities than wild cod. Captive cod fed different rations in the laboratory had condition factors between 1.1 and 1.8 with potential fecundities between 2 and 5.3 million eggs (fecundity for a standard 60 cm female). A wild cod of the same standard size had a condition factor of about 1 and a potential fecundity of 1.5 million. The extrapolation of results to wild cod, which generally exhibit lower condition factors and potential fecundities, has to be validated before derived equations are used to estimate the potential fecundity in wild populations. Long delays between capture and the observation of regular spawning in sole (Devauchelle *et al.*, 1987) may also indicate that laboratory determinations of potential fecundity are not comparable to field situations at least during the early years of captivity.

Direct measurements of realized fecundity may not be obtainable for wild fish (Lambert *et al.*, 2003) and for batch spawners like cod and haddock can only be obtained using tanks equipped with collectors (Hislop *et al.*, 1978; Kjesbu, 1989; Trippel, 1998; Trippel *et al.*, 1998; Lambert and Dutil, 2000; Thorsen *et al.*, 2003). Stripping of females may underestimate realized fecundity because manipulation during stripping and/or the timing of stripping in relation to ovulation time may result in the incomplete recovery of ovulated eggs (Buckley *et al.*, 1991; Norberg *et al.*, 1991). Potential fecundity of wild and captive fish appears to overestimate realized fecundity (Bromley *et al.*, 2000). Realized fecundity of American plaice in the laboratory was considerably lower than the potential fecundity in the wild (Nagler *et al.*, 1999), perhaps due to atresia and ovulatory failure. Laboratory experiments with cod indicated that realized fecundity was between 20 and 80% of the potential fecundity depending on the nutritional status of the fish (Kjesbu *et al.*, 1991). Oocyte atresia has even been associated with spawning failure in this species (Rideout *et al.*, 2000).

Determination of the level of atresia has been used as an indirect method of estimation of realized fecundity (Ma *et al.*, 1998). Many laboratory studies have examined the process of ovarian atresia and provided estimates of rates of atresia and duration of atretic follicles (Hunter and Macewicz, 1985; Kjesbu *et al.*, 1991; Ma *et al.*, 1998; Witthames *et al.*, 2000). The prevalence of atresia in sole from the Channel, the North Sea and the Irish Sea was also used to estimate realized

fecundity in the field (Witthames and Walker, 1995). Measurements of atresia in the laboratory and in the field could possibly be integrated to estimate the proportion of the potential fecundity in the wild that will effectively be realized. For example, a calibration using the atretic condition of the ovary of captive and wild northern anchovy (*Engraulis mordax*) was used to assess the reproductive state of this fish along the coast of California (Hunter and Macewicz, 1985).

Information on egg and larval characteristics (size, weight, energy, biochemical composition, etc.) has been obtained in the laboratory and in the wild (reviewed by Lambert *et al.*, 2003). However, most of the information on the relationship between egg and larval characteristics and their subsequent survival has been obtained with experiments on captive fish (Lambert *et al.*, 2003). Large variations in egg and larval traits, such as fertilization rate, egg survival, hatching rate and larval survival have been observed within and between studies (Manning and Crim, 1998; Trippel *et al.*, 1998; Ouellet *et al.*, 2001; Watanabe *et al.*, 2001; Lambert *et al.*, 2003). Greater variation in egg viability and fertilization rates seem to be observed in species that do not spawn naturally in captivity. In American plaice, the mean percentages of viable and fertilized eggs were 44.7% (11–71%) and 13.7% (0.2–49%), respectively (Nagler *et al.*, 1999). Viable eggs were defined as those having a distinct perivitelline space but no blastula formation, indicating that they were not fertilized. The number of larvae that hatched varied widely with a mean hatch success of 23% (Nagler *et al.*, 1999). Fertilization rates between 51% and 60% were observed for groups of female sole that spawned naturally (Houghton *et al.*, 1985; Devauchelle *et al.*, 1987). Higher egg quality of naturally spawning fish as opposed to hand-stripped fish, has been observed in turbot due to reduced stress and risk of physical damage (Bromley *et al.*, 1986). Natural spawning also has been reported to produce larger numbers of viable embryos than hormone-induced spawning and is less labour intensive and time consuming (Watanabe *et al.*, 2001). Proper timing of stripping in relation to ovulation markedly influences egg quality, fertilization and hatching rates (Hirose *et al.*, 1977). Stripping can disturb the ovulation process (Watanabe *et al.*, 2001) and over-ripening can cause rapid loss in egg viability. In turbot, hatching rates up to 97% observed in freshly ovulated eggs declined to 0% after 1 day of retention in the lumen of the ovary (McEvoy (Barton), 1984). Likewise, the fertilization rate of female snapper (*Parus auratus*) decreased to less than 50% after 6 hr of being retained in the oviduct (Hobby and Pankhurst, 1997).

The variability in egg size, egg dry weight, fertilization rate, and hatching success may be inherent to laboratory work. However, since little is known of spawning events in the wild, it is possible that the same variability is present in the wild (Bromley *et al.*, 1986; Manning and Crim, 1998).

Integration of experiments with captive fish

Influences of captivity on reproduction. The capture of wild fish for experiments on reproduction as well as routine husbandry procedures such as handling and confinement can be stressful to fish and may affect reproduction (Pankhurst and Van der Kraak, 1997). Stress can affect oocyte development and quality, as well as egg and larval survival and development. Increased amounts of atresia were observed in vitellogenic oocytes of wild mature female red gurnard (*Chelidonichthys kumu*) kept in tanks, indicating that capture and confinement stress can negatively affect their reproduction (Clearwater and Pankhurst, 1997). An increased incidence of ovarian atresia in wild and hatchery-reared snapper (*Pagrus auratus*) indicated that this species was highly susceptible to stress-induced impairment of reproduction (Cleary *et al.*, 2000). The lower incidence of atresia in hatchery-reared fish, however, indicated that hatchery fish were less susceptible to stress than wild fish. Stress induced by confinement also resulted in the production of smaller eggs in rainbow trout (*Oncorhynchus mykiss*) and a lower survival of the progeny occurred of stressed rainbow and brown trout (*Salmo trutta*) compared to unstressed fish (Campbell *et al.*, 1994). Chronic stress produced by chasing and capturing fish three times a week caused cod to produce greater numbers of abnormal larvae, but did not affect egg production, fertilization rate, hatching success or time to starvation of larvae (Morgan *et al.*, 1999). Extensive, but careful handling of Atlantic halibut showed no effect of manipulation on ovarian growth and ovulatory cycle (Norberg *et al.*, 1991). Likewise, handling stress produced by anaesthetising and injecting fathead minnow (*Pimephales promelas*) on three occasions before reproduction did not influence fecundity and hatching success (Kahl *et al.*, 2001). Adverse effects of handling may be reduced after several generations of culturing (Kahl *et al.*, 2001) and may differ between individuals (Norberg *et al.*, 1991).

Many physiological, haematological and physical condition indicators are used to monitor stress in fish. Blood glucose, cortisol, haemoglobin, hematocrit, white blood cells, ionic composition and condition indices are some of the variables commonly used as indicators

of stress (Morgan and Iwama, 1997). Abnormal behaviour, changes in colouration, and lesions to skin and fins also represent signs of stress and/or disease. Experiments with captive fish should include the measurement of some of these indicators. Experiments designed to measure responses to different levels of stress in the laboratory can be used to evaluate the susceptibility of different fish species to stress-induced impairment of reproduction. This information is important in extrapolating results on reproductive investment of captive fish to field situations.

Experimental conditions. Laboratory experiments designed to understand the reproduction of fish in natural environments should preferably use wild fish kept in captivity for limited periods of time. Fish should be captured before the onset of maturation to prevent the possible stress-related disruption of the maturation cycle. The use of domesticated fish should be avoided if possible. Selective breeding can lead to important differences in stress resistance, growth and reproduction between domesticated and wild fish (Pankhurst and Van der Kraak, 1997; Pottinger and Pickering, 1997).

Laboratory conditions never entirely mirror a fish's natural environment. However, holding conditions should mimic as closely as possible environmental conditions. Feeding schedule, ration and diet are of vital importance. Natural prey are preferred to formulated feeds and the quantity of food should be determined in order to obtain growth, maturation and reproductive effort in the range observed for wild fish. For example, cod fed on diets with a high lipid energy: total energy ratio will develop enlarged fatty livers which are considered abnormal for natural populations (Jobling, 1988). In many studies, feeding is stopped at the beginning of spawning (Kjesbu, 1989; Lambert and Dutil, 2000). This can ease manipulations and/or prevent problems with contamination (Manning and Crim, 1998). In many species, fish do not usually eat during the spawning period (Fordham and Trippel, 1999) but this may not be the case for all species (Hislop, 1975; Hislop *et al.*, 1978) or possibly for all conditions of a given species.

Sampling spawning females at sea can represent an alternative method to study and integrate egg and larval characteristics and survival measured in the laboratory to field situations, particularly for species that exhibit problems in acclimation to captivity. By sampling spawning female herring over a series of years at sea and incubating eggs, Laine and Rajasilta (1999)

were able to determine egg characteristics and viability in controlled conditions for females subjected to variations in environmental conditions during maturation. However, the results obtained with the eggs of batch spawners collected at sea could be more difficult to interpret if batch number, which influences egg characteristics (Hislop, 1975; Hislop *et al.*, 1978; Hinckley, 1990; McEvoy and McEvoy, 1992; Trippel, 1998; Ouellet *et al.*, 2001), is difficult to identify.

Experimental studies on egg and larval quality and survival have produced variable results. Handling stress during the course of reproduction, stripping, over-ripening, contamination of eggs, and infections caused by bacteria, protozoa and fungi can have marked effects on fertilization rates, hatch rates and survival (McEvoy (Barton), 1984; Manning and Crim, 1998; Nagler *et al.*, 1999). Nonetheless, many studies consider that this approach provides valid information on the reproductive performance of species in natural environments (Buckley *et al.*, 1991; Marteinsdottir and Steinarsson, 1998; Trippel, 1998; Laine and Rajasilta, 1999). Other studies admit to some reservations in extrapolating laboratory results to the wild. Benoît and Pepin (1999) hesitated to extrapolate hatching success results in yellowtail flounder from small static rearing containers to pelagic eggs in the wild. However, their results suggested that the pattern of hatching success would vary across temperatures encountered in the wild.

It is very important to ensure the repeatability of results from experimental work before extrapolation to field situations, especially for measurements of egg and larval quality and viability. Repeatability of experiments can be evaluated by comparing the results of more than one experiment with the same experimental protocol. Identical protocols and fish from the same stocks or eggs from the same females can be used in different laboratories to corroborate results.

Utility of laboratory studies. The determination of the reproductive potential of fish populations is important in analysing population dynamics. In that context, more precise estimation of egg production, not only in numbers but also in quality, is warranted. The integration of results on captive fish provides an opportunity by which estimation of the reproductive potential of fish populations may be improved. Laboratory work can greatly increase our knowledge of the factors and mechanisms regulating some aspects of reproduction, especially realized fecundity and egg and larval quality and viability. These reproductive char-

acteristics are not always easy to measure in the wild. The integration of captive and wild studies could be used to predict changes in egg production in response to changes in specific environmental conditions in the wild and to develop predictive models incorporating biological and environmental factors.

However, the application of experimental work on captive fish to situations in the wild is not straightforward. Some restrictions associated with the ability of fish species to adapt to captive conditions, their reproductive behaviour, and the experimental manipulations employed may limit the use of laboratory findings. Careful validation and calibration are necessary before extrapolating the results of experiments on captive fish to the wild.

Acknowledgements

We greatly appreciate the comments and suggestions made by two referees that led to improvement of an earlier manuscript draft.

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