Reviews in Fish Biology and Fisheries (2004) 14: 277–294

A review of the culture potential of spotted wolffish *Anarhichas minor* Olafsen

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Accepted 12 July 2004

Contents

Key words: aquaculture, biology, ecology, shallow raceways, spotted wolffish, *Anarhichas minor*

Abstract

The first articially fertilized spotted wolffish eggs hatched only 10 years ago, and today the species is considered a very promising candidate species for cold water aquaculture in the North Atlantic. Recent research has focused on identifying key biological parameters in spotted wolffish aquaculture in order to establish a full production line for the species, and basic aspects of reproduction and larval development are now understood, controlled, and no longer limiting production.

Spotted wolffish eggs (5–6 mm) have a protracted incubation period (800–1000 D°) and newly hatched individuals (20–25 mm) are well developed, with the only larval characteristic remaining being a relatively small yolk sac which is completely resorbed after 3–4 weeks. The species can be weaned directly on formulated feed, and high specific growth rates have been obtained in land-based culture facilities using shallow raceways. Adaptive immune responses are present early after hatching and few potential disease problems have been identified. Only one bacterial disease, atypical furunculosis, has been reported in farmed fish, but oil-emulsified vaccines have displayed efficient protection both in juvenile and adult fish. Ectoparasites may, however, constitute a problem during parts of the year when sea-water temperature increases.

Optimal temperature for growth decreases with increasing fish size and is 10–12 °C for early juveniles and 4–6 °C for adult fish and broodstock. Spotted wolffish is a very robust species, and juveniles thrive at high densities and may be reared at a wide range of salinity levels. The species has further displayed a high tolerance to environmental changes in water quality parameters such as oxygen, carbon dioxide and un-ionized ammonia. Currently, the possibility of rearing spotted wolffish in flat-bottom net cages with shelves in the sea is being investigated. Preliminary results suggest that sea-based production may be a viable alternative to land-based rearing of the species in certain areas.

Introduction

The aquaculture industry in the North Atlantic region has expanded extensively in the last decade, but has been dominated by the production of a few pelagic fish species. The aquaculture of bottom-living fish species has expanded at a far lower rate. At present, farming of bottom-living species is very space-demanding, as a traditional farm will need approximately 1000 m^2 of land for each 40 tons of yearly production. In addition, this production is labour-intensive, and often has inefficient logistic solutions for large-scale production. These constraints have clearly restrained diversification of the North Atlantic aquaculture industry into land-based farming of bottom-living species, which is currently limited to a moderate production of flatfish species such as turbot, *Scophthalmus maximus*, Atlantic halibut, *Hippoglossus hippoglossus*, sole, *Solea solea* and *S. senegalensis* and summer flounder, *Paralichthys dentatus* (Brown, 2002).

The spotted wolffish, *Anarhichas minor* (Olafsen), is an arctic-boreal bottom-dwelling species, distributed in the North Atlantic and the Barents Sea (Figure 1) (Østvedt, 1963). During the last

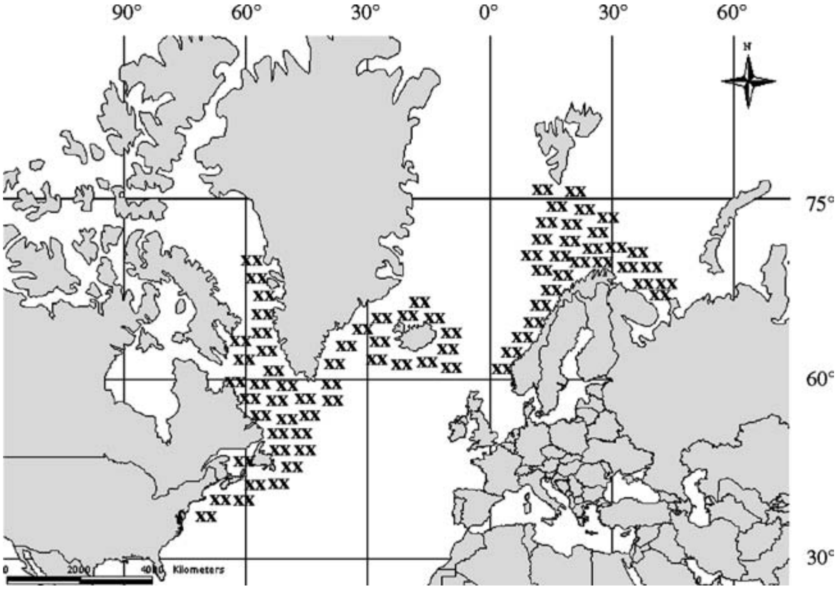

Figure 1. Distribution of spotted wolffish in the North Atlantic and Barents Sea.

decade, the species has emerged as a promising candidate for cold-water aquaculture, and is now looked upon with growing interest in Norway, Iceland, Canada, and Chile. The species has displayed a range of attractive characteristics for aquaculture purposes, including high specific growth rates in captivity, a non-aggressive behaviour and few disease problems. It was identified as one of the most promising species for cold-water aquaculture in Canadian waters when evaluated against specific biotechnical criteria (Le Francois et al., 2002). Due to its low temperature optima (< 10 °C), culture of the species in Norway, which so far is the only country where spotted wolffish is reared in commercial-scale facilities, has been restricted to land-based facilities pumping water from depths of stable low temperature.

Spotted wolffish is rather similar to the more southernly distributed common wolffish (*Anarhichas lupus*), but has been selected for aquaculture purposes due to higher growth rates (Figure 2), attainment of maturity at a larger size, a more husbandry-suited behaviour, more eggs per female and a higher fillet yield (Moksness, 1994). The nature of egg and larval development in the species, with hatching of well-developed, large fry ready to be fed on formulated food (Falk-Petersen et al., 1999; Hansen and Falk-Petersen, 2001a), has helped dodge some of the traditional bottlenecks often experienced in production of marine larvae, i.e. high mortality in the larval stage and obligatory initial feeding with live food items. Obstacles will, however, always emerge and in spotted wolffish a labour-intensive and space-consuming egg incubation period which lasts for several months, represents a vulnerable stage, where temperature fluctuations, mechanical disturbances and micro-organisms may cause high mortality and/or induce pre-mature hatching of the eggs (Pavlov and Moksness, 1993; Andreassen, 2000; Hansen and Falk-Petersen, 2001a). Research has, however, identified basic demands linked to reproduction, larval development, juvenile growth and diseases, and thus a complete production line has been established for the species in less than 10 years from when the first eggs were artificially fertilized

In 2004, it has been 10 years since the first artificially fertilized wolffish eggs hatched in experimental facilities, and in this review, we will present information on the work performed and progress made so far. We will systematize the knowledge accumulated by scientists working within various fields of expertise, in order to create a foundation for the future development of spotted wolffish aquaculture.

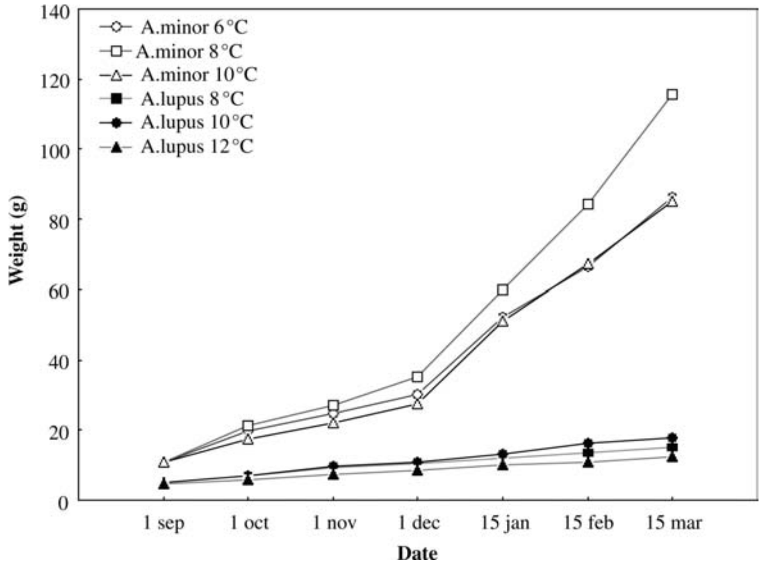

Figure 2. Growth of juvenile spotted and common wolffish at different temperatures. Spotted wolffish (open markers) at 6, 8 and 10 °C, and common wolffish (closed markers) at 8, 10 and 12 °C (Monsaas et al., unpublished data).

Biology of spotted wolffish

Life history

The wolffish family (Anarhichadidae) consists of only five species, of which two are found in the Pacific (wolf-eel, *Anarrhichthys ocellatus* and Bering wolffish, *Anarhichas orientalis*) and three in the Atlantic (spotted wolffish, common wolffish, and northern wolffish, *A. denticulatus*) (Eschmeyer et al., 1983; Masuda et al., 1984; Barsukov, 1986). The spotted wolffish is an arctic-boreal bottom-dwelling species, distributed in the North Atlantic and the Barents Sea (Figure 1) (Østvedt, 1963). It is found mainly in waters with temperatures ranging from −1 to 7 °C and at depths from 25 to 550 m (Barsukov, 1959).

The spotted wolffish is a typical benthophage, with teeth adapted to feeding on bottom-living organisms (echinoderms, molluscs and crustaceans) (Albikovskaya, 1982). In nature, growth is relatively slow (length increases approx. 10 cm/year until maturation) and maturation does not occur until after 7–9 years (females 1–2 years earlier than males) at a relatively large size (60–90 cm) (Barsukov, 1959; Østvedt, 1963; Templeman, 1986; Shevelev, 1988). Spawning occurs during late summer and early autumn and fertilization in the species is thought to be internal (Falk-Petersen et al., 1999). The female produces a large volume (c. 0.7–3.0 l) of eggs enveloped in a viscous gelatinous ovarian fluid (Kime and Tveiten, 2002). The eggs (5–6 mm diameter) are collected in a ball and probably guarded by the male until hatching, which occurs after approximately 800–1000 degree-days (D°) (Falk-Petersen et al, 1999; Hansen and Falk-Petersen, 2001a). The larvae hatch as well developed individuals (20–24 mm) with a relatively small yolk sac which is completely resorbed after 3–4 weeks. They feed and live pelagically for several weeks and settles in benthic environments at 4–6 cm length (Barsukov, 1959; Shevelev, 1994; Falk-Petersen et al., 1999).

Optimal temperature for growth and survival in the earliest juvenile phase (up to 60 days post-hatching, size 2–3 g) has been estimated to be 10.3 °C (Hansen and Falk-Petersen, 2002). Optimal temperature (T_{opt}) for subsequent growth decreases with increasing fish size, as T_{opt} for juveniles (10–500 g) is 8 °C and declines further to 4–6 °C for larger fish, including broodstock (Moksness, 1994; Lundamo, 1999; Kime and Tveiten, 2002). Spotted wolffish display higher growth rates compared to its relative, the common wolffish, as Moksness (1994) found that after 2 and then 3 years from hatching, spotted wolffish reached weights of 1.6 and 3.1 kg, while common wolffish only reached weights of 0.4 and 0.8 kg, respectively. In a growth study by Falk-Petersen et al. (1999), cultured spotted wolffish reached weights of 0.7, 2.7 and 5.1 kg after 2, 3 and 4 years, respectively.

Distribution and migrations

Spotted wolffish is commonly found in the Barents Sea, and is distributed in the eastern parts of the North Atlantic from Spitsbergen and Bear Island, along the coast of Finnmark in Northern Norway and as far south as Bergen (Figure 1) (Østvedt, 1963). The species is common in Icelandic and Greenlandic waters and along the North-American east coast from the Newfoundland and Labrador region southwards to the Gulf of Maine (Østvedt, 1963; Albikovskaya, 1982; Templeman, 1984, 1986). Tagging experiments have demonstrated that the fish undertake both short- and long-distance migrations (Østvedt, 1963; Templeman, 1984). Although the species in general is considered a slow-moving, inactive fish, tagging experiments have demonstrated migration distances of up to 5 nautical miles per day (Østvedt, 1963). It has not been determined if the fish undertake specific migration routes, but it has been suggested that a seasonal inshore-offshore spawning-related migration might occur, as Barsukov (1959) found a yearly variation in depth distribution of the species, with the maximum concentration of fish found between 100 and 150 m in August–October, and in deeper water throughout the rest of the year.

Fisheries

Wolffish tend to be widely distributed and are found in a broad range of depths. The species is mainly caught by line fishing, or as by-catches in other fisheries. In the North Atlantic, only common and spotted wolffish are caught for commercial fisheries, whereas the northern wolffish is discarded because of a jelly-like consistency of the flesh (Templeman, 1984). In the northwest Atlantic Ocean, Templeman (1984) reported that nominal catches of wolffish species (common and spotted) totalled 10,196 tons in 1981 (NAFO statistics), whereas landings in 2001 were reduced to 1659 tons according to the same source. Around Iceland, 1000–2000 tons of spotted wolffish are caught annually (G. Jónsson, Icelandic Marine Research Institute, pers. commun.) and in Norwegian waters, annual wolffish catches (common and spotted) have varied from 2100 to 16,300 tons (Department of Industry Statistics, Norway) in the years 1980–2003, with an average catch of 5700 tons per year. The fish are caught either by long-line fishing or as by-catches in other fisheries. The line fishing of the species takes place during spring and early summer (April–August) when the fish are located at feeding and mating grounds in the period before spawning (Østvedt, 1963).

Broodstock

Temperature

Optimal environmental conditions are an important prerequisite for successful cultivation of species in aquaculture, and temperature is the major factor influencing developmental rate in fish (Blaxter, 1988, 1992). So far, few studies have investigated the effects of temperature on the performance of spotted wolffish broodstock.

In general, broodstock of spotted wolffish is recommended to be kept at temperatures around 4–6 °C throughout the spawning season, although it is not yet fully understood how ambient temperature during final stages of maturation affects subsequent embryonic development and survival (Falk-Petersen and Hansen, 2003). Hansen and Falk-Petersen (2001a) compared survival and early development in spotted wolffish eggs and larvae as an effect of incubation temperature and female broodstock holding temperature. In their study, three females were kept at an average temperature of 6 °C while one female was kept at 9 °C at least 1 month prior to spawning. They found that eggs from the female kept at 9 °C did not differ from eggs from females kept at 6 °C with respect to survival, but the concluding material was limited and the lack of an effect could be attributed to genetic characteristics of the single female kept at a higher temperature. In common wolffish, on the other hand, Tveiten et al. (2001) investigated the effect of broodstock holding temperature during the breeding season (November–January) on final maturation and egg quality. They exposed adult fish previously held at 8 °C for several months to 4, 8 or 12 °C and found that temperature experienced by the adults affected egg development, even though eggs were incubated at a common temperature of 6 °C. The percentage of normally cleaved eggs and egg survival to the eye-stage were significantly lower at 12 °C compared to both 4 and 8 °C. Exposure to high temperatures (8 and 12 °C) also delayed ovulation compared to the 4 °C group.

Photoperiod

Fish, along with most other seasonally breeding animals, rely on cues from the external environment to achieve synchronization of maturation. Although a number of environmental factors have been implicated as possible cues, it is the seasonally-changing pattern of day-length which is probably responsible for the cueing and timing of reproduction in the majority of fish species (Bromage et al., 2001). Photoperiod manipulation is thus frequently used in finfish culture, and enables the farmer to manipulate maturation and spawning time. In this way a more stable year-round supply of eggs and fry, and a better exploitation of the rearing facilities, will be obtained.

At the facilities of Troms Steinbit AS (Troms county, northern Norway), successful shifts in spawning time have been obtained by exposing spotted wolffish broodstock to accelerated photoperiod regimes. A 3.5 months advance in spawning was obtained after approximately 18 months by exposing fish to two 9 month cycles representing 2 years (I. Andreassen, Troms Steinbit, pers. comm.) from June 1999 to January 2001. When compared to a control broodstock (natural photoperiod), spawning after 18 months in the manipulated group resulted in a lower percentage of fertilized eggs, a lower relative fecundity and smaller eggs, while no difference in egg survival (% fertilized) was observed (H. Tveiten, University of Tromsø, pers. commun). A reduced egg size in the first spawning season after two compressed year cycles could be expected, as advanced spawning generally results in smaller eggs (Bromage et al., 2001). The quality of the gametes in photoperiod-manipulated broodstock has, however, previously been shown not to be inferior from those derived from broodstock under ambient conditions, at least in salmonids (Bromage et al., 1992, 1993). In the case of the broodstock population at Troms Steinbit, it is uncertain why the percentage of fertilized eggs decreased among advanced spawners.

Apart from the commercial aspect of advanced or delayed spawning, i.e. year-round supply of eggs and juveniles and thus a more efficient exploitation of facilities, it could prove important to be able to steer the time of spawning into periods of the year when water temperature is optimal. As previously mentioned, spotted wolffish broodstock is recommended to be held at temperatures of 4–6 °C before and during the spawning season, and the ambient temperature at many localities, at least along the Norwegian coastline, may exceed this in large parts of the year.

To the authors' knowledge, no study has investigated the influence of light intensity and composition on spotted wolffish broodstock performance, or on any other life stage for that matter. It is generally accepted that the species prefer low light intensities with a deep water composition, and in most studies performed, whatever life-stage in question, light intensities applied have varied from almost total darkness (eggs) to 0.2–2 μmol m^{-2} s^{-1} (Lundamo, 1999; Foss et al., 2001; Hansen and Falk-Petersen, 2001a).

Spawning and fertilization

Maturing females of spotted wolffish are easily recognized by their bulging abdomens. The female produces a large volume of eggs enveloped in a viscous gelatinous ovarian fluid, of which the oocytes comprise 65–70% (Kime and Tveiten, 2002), and the fish should be stripped within 3–4 h after ovulation, which is characterized by the appearance of a wide genital opening (about 1 cm; Falk-Petersen et al., 1999). In captivity, males of spotted wolffish do not usually display normal spawning behaviour and the females will release unfertilized eggs (Kime and Tveiten, 2002). Thus careful monitoring of the maturity status of the females during the breeding season is required (Falk-Petersen et al., 1999). The eggs in the ovarian fluid are fertilized by undiluted sperm from at least two or three males, and then left for 2–3 h after stirring to ensure maximum fertilization. Male spotted wolffish produce very restricted amounts of sperm, varying from 0.5 to 6 ml, but good producers may often be stripped several times at weekly intervals during the reproductive season which can last for 3 to 4 months (Falk-Petersen and Hansen, 2003). Subsequently, eggs are transferred to seawater and gently stirred for the next couple of hours to prevent them from sticking together and thereafter carefully spread in a single layer in small upstream incubators to facilitate the tending operation (Falk-Petersen et al., 1999; Hansen and Falk-Petersen, 2001a, b, 2002; Falk-Petersen and Hansen, 2003).

Broodstock females, with weights varying from 3.6 to 13 kg have produced between 8000 and 30,000 eggs per season, and the fecundity of the females generally increases with increasing fish size. The pale yellow eggs are 5–6 mm in diameter and may vary in size between individuals, but egg diameter is not necessarily related to female fish size (Falk-Petersen et al., 1999). One of the most important aspects of stripping and fertilizing spotted wolffish eggs is to be able to select high quality egg batches for incubation based on systematized experiences from a number of egg groups. In some cases, late season spawners may produce over-ripe eggs of poor quality which in turn display low fertilization rates. Because of the labour-intensive task of removing dead eggs throughout the long incubation period, egg batches showing low fertilization rates should be discarded (Falk-Petersen et al., 1999).

It has been the general view, based on published literature on common wolffish (Johannesen et al., 1993; Pavlov, 1994; Pavlov and Moksness, 1996), that fertilization in the species is internal and occurs prior to spawning. This was supported by the findings of Kime and Tveiten (2002) who demonstrated that unlike most species, where an osmotic shock usually induces sperm motility (Morisawa and Suzuki, 1980), the sperm of spotted wolffish becomes immotile when mixed with seawater. This clearly indicates that this species does not release its sperm directly into the water during spawning. Kime and Tveiten (2002), however, raise some doubt over the question of internal fertilization in the species. They suggested instead that the male injects its sperm directly into the gelatinous egg mass as it is spawned, and then mixes it well during the early period of his incubation. They do not preclude, however, that eggs are fertilized internally before they become immersed in the protective gelatinous ovarian fluid.

Table 1. Embryonic development of *A. minor* at 8 °C and ontogenetic characteristics (from Falk-Petersen and Hansen, 2003)

Time/D°	Stage	Characteristics
6 h/2	Blastodisc	Cortical granules disappear
12 h/4	2-cell	Start of first cell-division
18 h/6	4-cell	
27 h/9	16-cell	
32 h/10.7	32- cell	
37 h/12.3	64-cell	
46 h/15.3	128-cell	
60 h/20	Mid-morula	
3.5 days/28	Start gastrula	
6.5 days/52	Gastrula	1/4 epiboly
10 days/80	Gastrula	3/4 epiboly
12 days/96	Organogenesis Embryo 2 mm	Blastopore almost closed, first somites visible
17 days/136	Embryo 3 mm	Brain divisions, otic and olfactory capsules, lenses, 30 somites, fin fold, fat globules in yolk fusing
22 days/176	Embryo 5 mm	Otoliths, heartbeats, blood cells, first movements, intestine, liver rudiment, pectoral fin rudiment, anal finfold, first hatching cells, fused fat globules
30 days/240	Embryo 8mm	Mouth opening, eye and body pigmentation noticeable, intestine pigmented dorsally, expanded posterior intestine with spincter, main yolk vitelline blood vessel, gill arches, urinary bladder, anus, pectoral fins, finfold complete
36 days/288	Embryo 8.5 mm (yolk 4.5 mm)	Eye pigmentation more noticable, weak body pigmentation, well pigmented intestine, pink blood, numerous hatching cells
44 days/352	Embryo 11 mm	Strongly pigmented eyes, 2/3 vitelline vascularization, folded intestine with expanded lumen, large liver, gall-bladder (green), urinary bladder
52 days/416	Embryo 13 mm	90% yolk vascularization, red blood, weakly pigmented head and dorsal body, dark intestine, dark particles in intestinal lumen, operculum, pectoral girdle, lower jaw well developed, (premature hatching may occur at this stage)
58 days/464	Embryo 15 mm (yolk 4.0 mm) (lipid 1.8 mm)	100% yolk vascularization, capillaries in fin fold, ray rudiments in tail and pectoral fins, peristaltic intestine, the 4 gill arches covered by operculum
65 days/520	Embryo 16 mm (yolk 3.4 mm) (lipid 1.7 mm)	50% fin rays in caudal- and 100% in pectoral fins, gill filament buds, gill rakers, jaws with teeth rudiments (increased frequency of premature hatching)

Table 1. Embryonic development of *A. minor* at 8 °C and ontogenetic characteristics

Time/D°	Stage	Characteristics
72 days/576	Embryo 17 mm (yolk 3.2 mm) (lipid 1.5 mm)	100% fin rays in tail, rays in ventral fin, yolk oblong, gill filaments, preanal finfold reduced, 6 pigmented rows on body, stomach, expanded urinary bladder
79 days/632	Embryo 18 mm	Head and ventral abdomen body more pigmented, olfactory clefts
86 days/688	Embryo 18.6 mm (yolk 3.0 mm) (lipid 1.4 mm)	Folded, intensily pigmented and more differentiated digestive tract and head region, dorsal fin rays formed, increased frequency of hyaline eggs (prematurely hatched embryos dead)
91 days/728	Embryo 20 mm	Increased pigmentation (both melanin and guanin)
97 days/776	Embryo 20.5 mm (yolk 2.5 mm) (lipid 1.2 mm)	A few hatched individuals, well-deeloped teeth, mouth and jaw, long gillfilaments
109 days/872	Embryo 21.5 mm (yolk 2.0 mm) (lipid 1.2 mm)	Some hatched individuals
116 days/928	Hatched 22 mm	Many hatched individuals and many hyaline eggs, gut highly twisted and expanded
122 days/976	Hatched 23 mm (yolk 1.4 mm) (lipid 0.7 mm)	Most embryos hatched, increased pigmentation on body (pigment bands pronounced)

Production of larvae and juveniles

Egg incubation

Several studies have investigated the effect of incubation temperature on survival, early development and growth in spotted wolffish. Falk-Petersen et al. (1999) incubated spotted wolffish eggs at fixed temperatures of 2, 4, 6 and 8 °C and at naturally decreasing, ambient sea-water temperatures (from 8 or 6 to 3 °C). They found that the number of day-degrees until hatching was influenced by incubation temperature, as eggs incubated at 4 and 6 °C hatched after 800–900 D °, whereas eggs incubated at 8 °C hatched after 940 D °. In their study, it was concluded that optimal incubation temperature was in the range 6–8 °C or at ambient, naturally decreasing temperatures for acceptable survival until hatching. In other studies (Hansen and Falk-Petersen, 2001a; T. Sund, University of Tromsø, unpublished data), best survival of eggs from fertilization until hatching was found in eggs incubated at 6 °C, compared to survival of eggs at 4 and 8 °C. However, in an additional study by Hansen and Falk-Petersen (2001b), it was found that survival until hatching was higher at 8 compared to 6 °C. Common in all those studies was the fact that eggs were collected from a limited number of females, thus a maternal effect, i.e. genetic variation among egg batches causing partly contradicting results, may be argued. Still, it is concluded by Falk-Petersen and Hansen (2003) that incubation at both 6 and 8 °C, as well as at ambient temperatures(6–8 °C decreasing towards hatching to about 3 °C) gives satisfactory survival during the incubation period. Furthermore, it is clear that incubation temperature affects survival and growth after hatching (Hansen and Falk-Petersen, 2001a). Eggs which had been incubated at 6 °C showed higher survival during initial feeding and subsequent growth. It is important to be aware of the fact that hatching is not a fixed developmental stage (as shown by Hansen and Falk-Petersen, 2001a). Embryos/larvae hatching from eggs incubated at 8 °C hatch at a premature stage (although at a higher number of D°) compared to those from eggs incubated at 6 and 4 °C, total mortality estimated during the encapsulated stage is not strictly comparable between temperature groups and do not reflect performance at later stages.

The embryonic development and ontogenetic characteristics of spotted wolffish in the egg incubation phase is described in Table 1. Mortality during incubation is generally highest during the first couple of weeks, and low or insignificant after the early eye-stage (c. 240 D°) in good egg batches (Falk-Petersen et al., 1999; Hansen and Falk-Petersen, 2001a). Several precautions may be taken in order to reduce mortality. As previously stated, it is clear that initial quality of the eggs significantly affects overall survival. Further, environmental disturbances such as swift temperature changes or short stops in water supply causing shortage of oxygen may result in premature hatching, and the eggs are also sensitive to mechanical disturbance during the early stages (Falk-Petersen et al., 2003).

Because of the protracted incubation period, micro-organism infections of spotted wolffish eggs represent a serious problem and repeated disinfection is a prerequisite for survival in culture (Falk-Petersen et al., 1999; Hansen and Falk-Petersen, 2001b). Up until now, eggs have been disinfected with glutaric dialdehyde at regular intervals, and different duration and concentrations have been tried. In common wolffish, Pavlov and Moksness (1993) recommended eggs be treated with a glutaric aldehyde concentration of 600 ppm for 5 min every third to fifth day during incubation. Hansen and Falk-Petersen (2001a) on the other hand, suggested that concentrations of 300 ppm and higher could have a negative effect on the hatching process, i.e. hardening of the egg shells and inhibition of hatching, and suggested a lower concentration be used. They found that best survival until hatching was obtained when eggs were disinfected twice monthly for approximately two-thirds of the incubation period at temperatures of 6 and 8 °C (Hansen and Falk-Petersen, 2001b). The percentage of pre-hatched larvae were, however, higher in eggs disinfected twice monthly, as compared to one treatment per month and the authors recommended that eggs should be disinfected once per month with glutaric dialdehyde (recommended dose 150 ppm for 5 min) for the first two-thirds of the incubation period. Due to the glutaric dialdehyde-related mortality observed in several experiments, various disinfectants are currently tested in Norway, accompanied by an increased focus on water treatment techniques in order to reduce the need for chemical treatments.

Weaning

The newly hatched larvae of spotted wolffish are 22–25 mm long and weighs from 80 to 110 mg (wet weight) (Falk-Petersen et al., 1999; Falk-Petersen and Hansen, 2003). The larvae apparently hatch as well developed individuals, with the only real larval characteristic remaining being a small yolk reserve, and are in most cases immediately active swimmers and positively photo-tactic (Falk-Petersen et al., 1999). Larval size and weight at hatch are greater among larvae from eggs incubated at 4 °C compared to those from 6 and 8 °C (Hansen and Falk-Petersen, 2001a). Shortly after hatching, the larvae are moved to short, low water-level (~1.5 cm) raceways (~ 15 × 30 cm, Figure 3) and weaned, where they start feeding within the first few days (Falk-Petersen et al., 1999; Falk-Petersen and Hansen, 2003). Due to the physical properties of

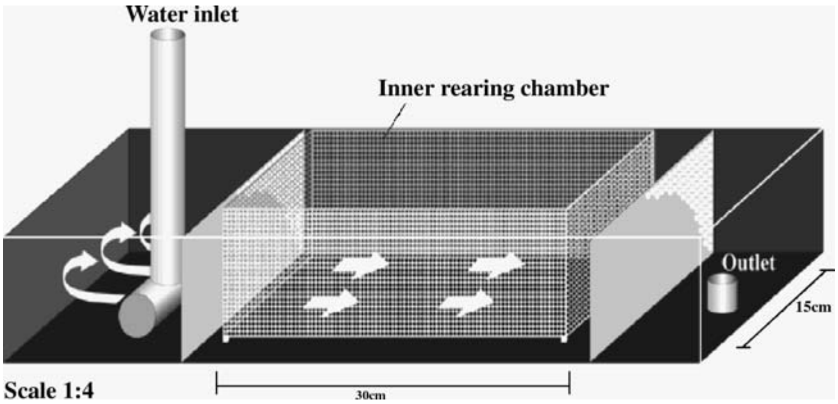

Figure 3. Raceway design (from Hansen and Falk-Petersen, 2002).

the raceways, i.e. low water level, large surface area and downstream current, it is important that floating food particles are used. This way the current will distribute food particles downstream from the point of water entrance and thus ensure proper feeding of all individuals in the raceway. The larvae can be start-fed on various feed types. Falk-Petersen et al. (1999) used live feed (*Artemia* nauplii) for about 3 weeks followed by dry feed (300–500 μm and later 500–800 μm granules), whereas Hansen and Falk-Petersen (2002) offered first-feeding larvae with two different types of formulated start-feed (250–1000 μm granules) containing 60% protein and 20% lipid (type 1) and 60–62% protein and 16–18% lipid (type 2). The latter study resulted in high growth and survival rates when using any of the feed types, and weaning on live organisms may thus be omitted. In commercial production facilities in Norway, only formulated feed is used. Beyond the weaning period (3–4 weeks after hatching), mortality is very low.

Early growth and survival

Of all environmental factors that influence growth in fish, temperature is the single most dominant (Brett, 1979). In juvenile spotted wolffish, growth rate is significantly influenced by temperature, and seems to follow a pattern typical of most fish species. This pattern is characterized by a rapid increase in growth rate as temperature increases, a peak signalling the optimum temperature for growth ($T_{\mathrm{opt}}G$), and frequently, a precipitous decline as higher temperatures become adverse beyond $T_{\mathrm{opt}}G$ (Brett, 1979; Imsland et al., 1996). This growth pattern was demonstrated clearly, at least in the very early juvenile stage, in spotted wolffish by Falk-Petersen et al. (1999) and Hansen and Falk-Petersen (2002). In the former (1999) study, newly hatched larvae were reared at 4, 6 and 8 °C, and growth was found to increase with increasing temperature during the first 48 days after hatching. In their later (2002) study, two experiments were performed. In the first, newly hatched larvae were reared at ambient temperature (2.9–4.5 °C) and at 6, 8, 10 and 12 °C. During the first 63 days, growth rates increased with increasing temperature in this experiment (SGRs from 1.8% day^{-1} at ambient temperature to 3.1 and 4.7% day^{-1} at 6 and 12 °C, respectively). In their second experiment, set up to detect potential detrimental temperatures, fish were reared at 8, 10, 12, 14 and 16 °C for 30 days, and all groups were then reared at a constant temperature of 8 °C for an additional 33 days. After 63 days, mean wet weight increased with increasing temperature from 8 to 14 °C, whereas fish reared at 16 °C performed significantly poorer compared to all other groups, indicating that $T_{\mathrm{opt}}G$ was passed and that 16 °C represented a sup-optimal temperature for spotted wolffish larvae.

The aforementioned experiments clearly demonstrate a strong temperature-growth relationship in early juvenile spotted wolffish, but this relationship is only valid for surviving individuals. In the study of Falk-Petersen et al. (1999) best growth was obtained at 8 °C, whereas overall survival was highest at 6 °C. Similarly, in Hansen and Falk-Petersen (2002, exp. 1) best growth was obtained at 12 °C, while survival was lower at this temperature compared to all other groups. In the second experiment, best survival was obtained at 8 °C (64%), whereas only 25% of the fish survived in the group displaying highest growth rates (14 °C; Figure 4). At 16 °C only 2% of the fish survived to day 63 post-hatch. Overall, the optimal temperature with respect to growth and survival during the weaning phase (first 63 days after hatching) was calculated to be 10.3 °C (Figure 5, Hansen and Falk-Petersen, 2002).

Environmental conditions – juvenile growth

Temperature

A common finding in studies examining the relationship of temperature and size on growth is that $T_{\mathrm{opt}}G$ shifts to lower temperatures as fish increase in

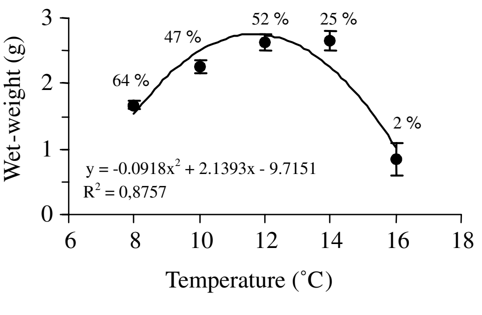

Figure 4. Mean weight (g) and mean survival (%) of spotted wolffish larvae at 63 days post hatch fed at constant temperatures (8, 10, 12, 14 and 16 °C) until 30 days post-hatch, thereafter slowly regulated to constant 8 °C for the next 33 days (from Hansen and Falk-Petersen, 2002).

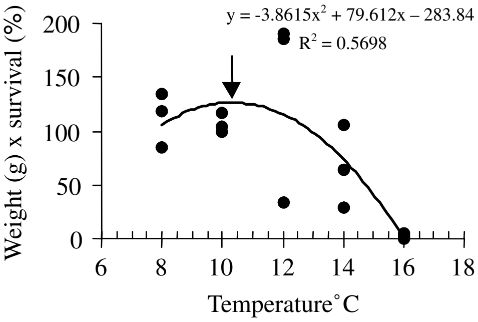

Figure 5. Growth and survival of first feeding spotted wolffish larvae at constant temperatures (8, 10, 12, 14 and 16 °C) until 30 days post-hatch, thereafter slowly regulated to constant 8 °C for the next 33 days. The arrow indicates the calculated optimal temperature (10.3 °C) for both growth and survival (from Hansen and Falk-Petersen, 2002).

size. Such a decrease in $T_{\mathrm{opt}}G$ with increasing size has been shown for juvenile halibut (Björnsson and Tryggvadóttir, 1996; Jonassen et al., 1999) along with several other marine species (plaice, Fonds et al., 1992; turbot, Imsland et al., 1996), and has been demonstrated for fish in general (Cuenco et al., 1985). Few studies have, however, systematically investigated the effect of temperature on spotted wolffish growth performance during the juvenile growth phase. In an experiment performed at the facility of the Norwegian College of Fishery Science, spotted wolffish with a mean start-weight of 4 g were reared at 6, 8 and 10 °C. In this study it was found that in fish ranging from 4 to 35 g, growth was highest at 8 °C (A. K. Monsås, pers. commun). Moksness (1994) indicated that optimal temperature for growth in spotted wolffish in the juvenile growth phase was lower than 7 °C, and in a study by Lundamo (1999), comparing growth in spotted wolffish with start-weight 720 g and exposed to both ambient temperature (3.5–6.5 °C) and stable temperatures at 6 and 8 °C, it was indicated, although differences were non-significant, that a temperature of about 6 °C was optimal for fish of that size. Falk-Petersen et al. (2003) further recommended that broodstock fish (> 4 kg) should be kept at a temperature as low as 4 °C, thus a downward shift in $T_{\mathrm{opt}}G$ with increasing fish size is evident in spotted wolffish.

Photoperiod

A general growth-promoting effect of extended photoperiods or continuous light have been recorded in several species. In juvenile Atlantic salmon (*Salmo salar)* (e.g. Stefansson et al., 1989; Solbakken et al., 1994), and Pacific salmonids (*Oncorhynchus* spp.) (e.g. Clarke and Shelbourn, 1986) a growth-promoting effect of long photoperiod has been demonstrated. The same seems to be the case for marine species (Boehlert, 1981; Folkvord and Otterå, 1993; Imsland and Jonassen, 2002), although the response does not appear as pronounced as that observed in salmonids. In spotted wolffish (mean start weight, 47 g), Jonassen (2002) did not find that continuous light (LD24:0) gave faster overall growth compared to short day-lengths (LD8:16). In a study by Lundamo (1999), spotted wolffish (110 g) were reared for 24 weeks at three different photoperiod regimes; LD24:0 for 24 weeks, LD24:0 transferred to LD8:16 after 6 weeks, LD24:0 transferred to LD8:16 after 6 weeks and back to LD24:0 after 15 weeks. In her study, fish transferred from continuous light to short day-length after 6 weeks displayed higher mean weights compared to the other two treatments at the end of the experiment. The difference could be attributed to a significantly higher growth rate in this group during the final 9 weeks of the experiment. During this period (simulated summertime), temperature increased, and it is possible that exposure to continuous light, generally resulting in a higher activity level, combined with a supra-optimal temperature, affected those fish negatively.

Salinity

Spotted wolffish is considered a typical stenohaline marine teleost, as in its natural habitat it experiences minor fluctuations in both temperature and salinity. Even so, it is well known that teleost fishes regulate their plasma ions so that the internal osmotic pressure of their body fluids is equivalent to *c.* 10–15‰ salinity (Brett, 1979). Accordingly, marine fish species expend energy to meet the metabolic cost of ionic and osmotic regulation (Brett, 1979; Jobling, 1994), and it has been hypothesized that growth and food conversion might be improved in an iso-osmotic environment. The studies of Lambert et al. (1994), Gaumet et al. (1995), Woo and Kelly (1995) and Imsland et al. (2001) have demonstrated beneficial effects on growth performance of marine fishes reared at salinities lower than that of full strength seawater.

Foss et al. (2001) reared juvenile spotted wolffish at salinities ranging from 12 to 34‰ for 12 weeks and demonstrated that the species has a strong osmoregulatory capacity and thus could be reared at a wide range of salinity levels. In the above study, no overall significant growth differences were found among groups, although there were indications that intermediate salinities resulted in better growth and food conversion efficiency. In the closely related common wolffish, Le François et al. (2004) found a growth promoting effect from rearing juveniles at 14‰ compared to 28‰. In an aquaculture context, these observations may be transformed into practical application, as two thirds of the water needed for farming can be extracted from freshwater reservoirs like lakes, rivers or aquifers.

Stocking density

Stocking density is an important aspect of commercial-scale aquaculture. High stocking densities have usually been reported to have negative effects on feeding and growth in fish (e.g. Holm et al., 1990; Björnsson, 1994). In large scale facilities, however, a certain reduction in individual growth rates may be accepted if the growth loss at high densities is compensated for by an overall larger biomass increment than at low densities.

In Norway and Iceland, spotted wolffish are commonly reared in shallow raceways, a system designed for carrying high densities of fish. The shallow raceway will often operate with densities per square meter equal to those used in traditional tanks, but the density per cubic meter will be far higher. For instance, spotted wolffish (70 g) reared in raceways for 12 weeks had an initial/final stocking density of 27/40 kg m^{-2}. Water level in that study was, however, only 10 cm, thus measured in cubic meters, initial/final stocking density was 270/400 kg m^{-3} (A. Foss, unpublished data), which is fairly high.

In general, spotted wolffish seem to prefer the company of others and thus to be densely packed, as the fish usually gathers in clusters when density is low (Øiestad, 1999; pers. obs.). However, Jonassen (2002) demonstrated that increased stocking density led to reduced growth also in spotted wolffish. When fish (460 g) were reared for 126 days at two stocking densities, final mean weight was 10% higher in fish reared at 25 kg m^{-2} compared to 40 kg m^{-2}. The experiment of Jonassen (2002) was, however, performed in square tanks with a static number of fish, thus fish density increased throughout the experiment. In another experiment, larger (1.5–3 kg) fish were reared in shallow raceways at densities of 70, 110 and 150 kg m^{-2} (210, 330 and 450 kg m^{-3}, respectively, J. Solbakken, Akvaplan-niva, unpublished data). In that experiment, densities were held constant by gradually increasing the residence area of the raceway. Specific growth rates were found to decrease with increasing stocking density, and it was recommended that stocking density for fish of this size should not exceed 70 kg m^{-2}. Still, biomass increase was higher in the two high density groups, thus a growth loss at high densities may be compensated for by an overall larger biomass increment than at low densities. A similar result has previously been demonstrated in Atlantic cod (Lambert and Dutil, 2001).

Nutritional requirements

The nutritional requirements of juvenile spotted wolffish have not been thoroughly investigated. In general, protein-rich feed (55–62%) have been used, but good growth rates have also been obtained using feed with a lower (45–50%) protein content. Jonassen (2002) investigated growth in juvenile spotted wolffish (450 g) fed one low fat (15%) and one high fat (20%) diet. He demonstrated a negative relation between dietary fat level and growth as fish in the low-fat group had a 13% higher final mean weight at the end of the experiment compared to fish on a diet with 20% fat.

Growth is of course the primary factor considered when developing formulated feed for cultured organisms, but the general composition of the feed may also have an effect on the organism in question. Foss et al. (2003a) found calcareous deposits, i.e. nephrocalcinosis, in the kidneys of juvenile spotted wolffish in an experiment where the fish were exposed to various degrees of environmental hypercapnia (chronic carbon dioxide exposure). Nephrocalcinosis was, however, also observed in the control group, and in several fish prior to hypercapnic exposure, indicating that other factors were, at least partly, responsible for this condition. Some studies have demonstrated that the prevalence of nephrocalcinosis in fish is not necessarily caused by water carbon dioxide content, but could also be attributed to dietary factors, e.g. selenium toxicity (Hicks et al., 1984), magnesium deficiency (Knox et al., 1981) and a generally unbalanced food mineral content (Hilton and Hodson, 1983). It is therefore possible that the food currently used in spotted wolffish culture does not hold the ideal mineral composition for this species.

Diseases

Infections caused by bacteria, viruses and parasites are a common problem in farmed fish. In spotted wolffish, being a relatively new species for cold water aquaculture, an important tasks has been to investigate the susceptibility of the species to various types of diseases and then to develop vaccines. This activity was initiated early on by Norwegian scientists. Susceptibility studies were performed by experimentally infecting spotted wolffish with various fish pathogens, and a surveillance program of commercially farmed wolffish was started.

Viral diseases

Infectious pancreatic necrosis virus (IPNV) and nodavirus (NV) have caused mortalities in several farmed marine species, e.g. Atlantic halibut (Grotmol et al., 1997) and Atlantic cod (Starkey et al., 2001), and could be expected to cause problems also in the culture of spotted wolffish. Nodavirus causes viral encephalopathy and retinopathy (VER), but natural outbreaks of VER have not yet been reported in wolffish (Johansen et al., 2003). The studies of Sommer et al. (2004) and Johansen et al. (2003) did, however, both demonstrate that young spotted wolffish were indeed susceptible to infection with a nodavirus isolated from Atlantic halibut, and the fish developed classical signs of VER following experimental bath challenge. In the study of Johansen et al. (2003), nodavirus was re-isolated from eyes, brain and abdominal organs 16 weeks post-challenge in surviving fish, demonstrating the presence of an infectious virus which might spread from sub-clinical nodavirus-infected wolffish to other co-specifics.

Bacterial diseases

The only bacterial disease registered in spotted wolffish is atypical furuncolosis. Atypical furuncolosis is caused by atypical *Aeromonas salmonicida* and is an increasing problem in commercial halibut farming, and represents a potential problem in farming of spotted wolffish (Ingilæ et al., 2000). The bacteria are reported to be very heterogeneous in terms of molecular and phenotypic characteristics, and the variations are not only observed between strains from different fish species, but also between different strains from one particular species (Lund et al., 2002, 2003). Experimental oil-adjuvanted vaccines that resulted in high protection after challenge, have been developed for spotted wolffish (Ingilæ et al., 2000; Lund et al., 2002). Injections of oil-adjuvanted vaccines demands, however, that the fish have reached an adequate size for handling, and immersion vaccines are thus often a preferred alternative. Grøntvedt et al. (2004) found that immersion vaccination of wolffish juveniles in an atypical *A. salmonicida* bacterin was not efficient as prophylactic treatment against atypical furunculosis.

Parasitic diseases

Parasitic diseases have so far been proven to represent the most severe problem in spotted wolffish culture. The ectoparasites *Ichtyobodo necator* (Costia) and *Trichodina* sp., which attach themselves to gills and skin, especially in juvenile fish, are the most common (Grøntvedt, 2003). Treatments of these parasitic infections with formalin have proven effective, but more gentle treatment methods should be developed as an alternative. In very early juveniles, filtration and UV treatment of the rearing water have reduced the problem with parasitic diseases (Falk-Petersen et al., 2003). The parasites *Gyrodactylus* sp. and *Pleistophora* sp. have been observed in larger fish, but still to a limited extent. The intracellular *Pleistophora* sp., that infects muscle cells, can cause large abscesses in the tissue and thus reduce the quality of the fish (Falk-Petersen et al., 2003).

Experiences so far indicate that spotted wolffish is very robust and few potential disease problems have been detected. The larvae hatch with well developed organ systems, and adaptive immune responses are present early after hatching (Grøntvedt, 2003). The species has displayed low susceptibility to viral and bacterial pathogens, and only one bacterial disease, atypical furunculosis, have been reported in commercial facilities. Vaccines have, however, provided efficient protection against this disease among both juvenile and adult fish.

Culture systems to maximize growth

Shallow raceways

Optimum temperatures for growth and survival in spotted wolffish at various life stages ranges from 4 to 12 °C (Moksness, 1994; Lundamo, 1999; Hansen and Falk-Petersen, 2002). As the North-Atlantic coastal waters may experience large temperature fluctuations throughout the year, the species are, as of today, best suited for land-based farming. High construction and operational costs of such facilities requires effective utilization of pumped water, and shallow raceways in racks with reuse of water between levels will effectively reduce the overall logistic needs with respect to buildings and water supply systems, and also, through its compactness and extended automation, simplify the operation in the production process (Øiestad, 1999). The shallow raceway will often operate with densities per square meter equal to those used in traditional tanks, but the density per cubic meter will be far higher. This might seemingly cause new challenges, but observations indicate that the shallowness might represent an important improvement for animal welfare. Observations indicate that fairly high densities are preferred by fish in captivity, and it has been noted that flatfish reared in more than one layer are more resistant to stress and disturbance as they serve as a sand substitute for each other (Lyngstad, 1994). The shallowness also prevents overcrowding of particular areas, and the strong turbulence causes continuous water renewal around the fish. The current also distributes floating pellets downstream from the point of water entrance, a necessity for this system to function as intended. In traditional tanks the fish will leave the bottom and hunt for food, and thus feeding hierarchies may easily form, where one or a few high-ranked fish monopolize the food resources at the expense of lower-ranked individuals (Jobling and Koskela, 1996). With no arena for food struggle, these forces may operate to a far lesser extent in a shallow raceway. Consequently every fish has a similar opportunity to catch food pellets, and food consumption per kg fish may be higher in shallow raceways than in traditional tanks, which may in turn increase overall food conversion efficiency. An optimized raceway system with reuse of water between racks might reduce land use to 20% of traditional tank farming facilities and reduce seawater need to 5% of that used by a normal flow-through system.

Sea cages

In Norway, a project consortium is currently investigating the possibilities of rearing spotted wolffish in sea cages (L.O. Sparboe, Akvaplan-niva, pers. comm.). The system tested is flat-bottom net cages (PolarCirkel AS) with shelves, modified from similar cage systems commonly used for sea-based culture of Atlantic halibut. Production of spotted wolffish in such cages will make specific demands on both location and technological solutions. The surface layer of Norwegian coastal waters experience large temperature fluctuations throughout the year, with surface waters in the southern regions exceeding 20 °C during summer, thus suitable locations with surface waters of stable, low temperature ($t < 12$ °C), are primarily found in the northernmost parts of Norway (the Troms and Finnmark county). Based on experiences from land-based culture, where spotted wolffish often let themselves drift with the flow if the current in the rearing unit is too high, it is assumed that a net-cage facility should be located on low-current locations. It is further expected that movements of the cage bottom, caused by wind and waves, will affect the fish negatively and reduce animal welfare and appetite, thus shielded locations are preferred. Last, but not least, the cages must be protected from the sun, as severe sunburn have been observed in fish during summer. In the on-going experiments, where fish of different sizes have been transferred to sea cages at different times of the year, the consortium is investigating growth and monitoring behaviour of the fish, as well as documenting characteristics of the sea cages. The purpose is to develop a concept for sea based culture of the species, including both logistic and operational aspects of net cage farming.

Water quality requirements

High construction and running costs of intensive land-based facilities require effective utilization of pumped water. Fish densities may be very high in such rearing systems, and one might experience significant drops in water pH and dissolved oxygen content, along with an accumulation of natural catabolites such as ammonia and carbon dioxide (Person-Le Ruyet et al., 1997). These parameters may separately or together affect production characteristics, and must be taken into consideration in order to optimize rearing conditions, and thus prevent water quality from acting as a limiting factor for optimal growth and welfare of the fish. Detailed knowledge on the impact of water quality factors on basic production characteristics such as growth performance, food conversion efficiency and fish welfare is therefore needed in order to exploit such hyper-intensive farming systems effectively.

In spotted wolffish, a series of experiments have recently been carried out in order to map the environmental water quality requirements of the species (Foss and Imsland, 2002; Foss et al., 2002, 2003a, b, c). In those experiments, the impact of such parameters as oxygen saturation (hyperoxia and hypoxia), un-ionized ammonia (UIA) and carbon dioxide were investigated. The results demonstrated that spotted wolffish is very tolerant to persistent environmental changes in water oxygen content (Foss et al., 2002, 2003b). When exposed for 11 weeks to oxygen levels of 4.0, 6.0, 9.6 and 14.5 mg O_2 l^{-1}, it was demonstrated that after a period of acclimation, the fish performed equally well at O_2 saturations ranging from 6.0 to 14.5 mg O_2 l^{-1} (Foss et al., 2002). It was further demonstrated that juvenile spotted wolffish displayed a period of compensatory growth when transferred from hypoxic to normoxic conditions (i.e. 9.6 mg O_2 l^{-1}) (Foss and Imsland, 2002). This growth spurt mechanism might be applied for aquaculture purposes, as appropriate exploitation may result in an overall increase in growth and food conversion efficiency. Foss et al. (2003c) investigated the effect of chronic exposure for 69 days to UIA on growth in the species, and found that UIA concentrations of 0.13 and 0.25 mg l^{-1} reduced mean weights in the fish by 13 and 40 %, respectively, compared to the control group. Besides, a positive interactive effect of oxygen and ammonia content was found, i.e. tolerance to UIA seemed to increase in spotted wolffish reared at hyperoxic compared to normoxic conditions (Foss et al., 2003b). In the study where Foss et al. (2003a), focused on the species tolerance to environmental hypercapnia, juvenile spotted wolffish were exposed to carbon dioxide ($CO_{2(aq)}$) concentrations of 1.1 (control), 18.1, 33.5 and 59.4 mg l^{-1} for 10 weeks. In that study, no significant reduction in growth performance was seen up to a level of 33 mg CO_2 l^{-1} (pH 6.7). Still, the results suggested that the occurrence of nephrocalcinosis could occur at lower levels.

From the findings of Foss and colleagues it can be concluded that spotted wolffish in general is a relatively hardy species and tolerant to persistent changes in water quality. It has previously been mentioned that spotted wolffish is a strong osmoregulator as it can be reared at salinities ranging from 12 to 34 ‰ without compromising growth (Foss et al., 2001). That, together with the above findings, may be transformed into practical application, as two-thirds of the water needed for farming could be extracted from lakes, rivers or ground-water reservoirs with less pumping involved. Use of oxygen supersaturated water may further reduce pumping costs, and may also increase spotted wolffish tolerance to un-ionized ammonia. The regions suited for spotted wolffish culture could also be extended geographically, as marine ground-water resources of constant low temperature and salinity might be utilized in areas where seasonal seawater temperature fluctuations prevents culture of the species.

Conclusions

Spotted wolffish is a new and promising candidate for cold water aquaculture because of its fast growth and its unique farming-friendly behaviour. Ten years ago the first artificially fertilized spotted wolffish eggs were hatched and in 2004, between 50 and 100 metric tons will reach the Norwegian restaurant market with further increase expected in subsequent years. The high market price (8–12 € kg^{-1}) obtained by the farmer and a very high filet gain compared to wild specimens due to a high condition factor, will make farming profitable. The species is now studied in pilot scale in Iceland and Canada with commercialization as the main purpose.

The current review has described the main efforts undertaken so far, where particular focus have been on both identifying key aspects of egg and larval rearing and environmental optimization in the early juvenile phase and on water quality aspects during juvenile growth. No biological or technological bottlenecks associated with spotted wolffish culture remain, and the species is thus ready for industrial up-scaling. There is, though, still a need for further industrial development to streamline the production, and more species-specific market research before spotted wolffish can attain its full potential as a cultured species. Farming is still restricted to areas where water of stable low temperatures can be found throughout the year, i.e. the northern-most areas, but this is expected to change over time. Besides, the species is still rather unknown among the general public outside some few markets.

Continued commitment from scientists, commercial companies and investors will be necessary in order to develop a solid technological–biological basis for sustainable aquaculture of the spotted wolffish. Significant effort is still needed in the areas of scaling-up egg and larval production in order to reduce the price of juveniles, now being 3–4 €, broodstock management, fish health, stock- and species-specific genetic studies and development of selective breeding programmes to reduce production time, which currently is about 3 years for a 3–4 kg fish.

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