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Diet and size-selective feeding by escaped hatchery rainbow trout *Oncorhynchus mykiss* (Walbaum)

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Escaped hatchery rainbow trout, *Oncorhynchus mykiss* (Walbaum), at post-smolt (120–340 g) and adult stages (800–3400 g) adapted differently to natural marine prey after escaping from two fish farms in northern Norway. About 1 month after escape (July), more than 57% of the post-smolt fed actively on fish larvae, which contributed 63–75% of the diet by weight. Surface insects were consumed by more than half the post-smolts and represented 24–48% of the diet during the 3-month period of sampling (June–August). One month after escaping, forage ratios (weight stomach/weight fish × 100) exceeded 1, similar to ratios recorded for other wild anadromous salmonid species in the area. Post-smolt weight increased during the sampling period and the condition factor was stable. In contrast, the condition factor of escaped adult fish reduced significantly and the forage ratios were consistently low (0.05–0.77) during the 15 months of sampling (March–August) following their escapement. These fish fed primarily on a variety of different indigestible items (especially particles of seaweed and small pieces of wood) that contributed about 70% of the stomach content weight. They took fish larvae only in July. Although generally contributing little to their overall diet, marine prey of great variety was consumed by the adult fish. The results indicate that young domestic rainbow trout more easily adjust to natural feeding after escape than the older, larger fish, which often fed on indigestible items similar in shape to the commercial pellets to which they were accustomed.

Keywords: aquaculture, diet, escapees, fish farm, hatchery, interactions, steelhead.

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Introduction

In recent years, Norwegian hatchery production of rainbow trout [*Oncorhynchus mykiss* (Walbaum)] has increased rapidly, and now represents almost one-fifth of the total production of salmonids in sea cages in 2002 (220 million fish, Statistics Norway, www.ssb.no). Coincident with the increased production is a greater number of rainbow trout escapees. In 2002, more than 220 000 fish were reported lost, approximately 36% of all escaped salmonid hatchery fish in Norway (statistics, www.fiskeridir.no). Escapements result in substantial economic loss to the industry, but also represent a potential threat to wild fish stocks, especially because rainbow trout is an introduced species not only in Norwegian waters, but also in other countries around the North Atlantic (Jonsson *et al.*, 1993a; Hindar *et al.*, 1996; Landergren, 1999; Porter, 2000).

Spawning of anadromous rainbow trout has been observed in several Scandinavian watercourses (Jonsson *et al.*, 1993a; Hindar *et al.*, 1996; Sægrov *et al.*, 1996; Landergren, 1999). To date, however, this has not resulted in the establishment of any persistent local populations of the species (Landergren, 1999). The reasons for this are unclear, but they might include factors such as low resistance to European parasites, competition with other species, environmental conditions, genetic drift, and selection during domestication (Hindar *et al.*, 1996; Volpe *et al.*, 2001; Alvarez and Nicieza, 2003; Weber and Fausch, 2003). However, the possibility of successful establishment may increase with increasing numbers of rainbow trout entering the same rivers over several years (Hindar *et al.*, 1996; Ricciardi, 2001; Perez *et al.*, 2003).

One aspect that may influence the possibility of successful spawning of escaped hatchery rainbow trout is their ability to adjust to natural feeding at sea. For example, if a rainbow trout escaped at the post-smolt stage it would have to feed adequately on natural prey in order to grow and attain sufficient energy required for maturation later in life (Thorpe *et al.*, 1998; Rikardsen *et al.*, 2004b). Experimental studies of Atlantic salmon *Salmo salar* L. have shown that hatchery-reared fish trained to feed on live prey before release have a better chance to survive, feed, and grow at sea than those fed only on pellets (Brown *et al.*, 2003a, b). Post-smolt hatchery Atlantic salmon released for cultivation purposes fed significantly less in their early marine phase than their wild companions (Sturlaugsson, 1994, 2000). However, later in their marine life, both cultivated and escaped hatchery salmon grew and adapted well to marine prey, often feeding at similar levels as wild fish (Jacobsen and Hansen, 2001; Jonsson *et al.*, 2003). Jonsson *et al.* (1993a, b) showed that hatchery-reared 1+ and 2+ rainbow trout released for sea ranching purposes in Norway grew, but that growth was inversely related to size at release. Some fish returned after spending up to 3 years at sea, indicating that hatchery rainbow trout that have escaped from sea cages may have the capacity to survive and adapt to marine prey. However, to our knowledge, there is no information on the marine feeding habits of escaped hatchery rainbow trout in European waters.

For this study, stomach samples were examined from hatchery rainbow trout that escaped as post-smolt (1+) and adults (2+) in two Norwegian fjords. Samples were obtained between 1 month and several months after escape (i) to evaluate if and when the fish adjust to live prey, and (ii) to determine if size and age at escape influence their subsequent feeding habits.

Material and methods

The study was conducted in two fjords in northern Norway: Sagafjord (Steigen municipality) (67°54′N 15°20′E) and Altafjord (70°05′N 22°55′E). During mid-May 2002 in Altafjord, an unknown number of post-smolt (120–340 g) rainbow trout escaped from a local fish farm shortly after transfer to saltwater. On 8 February 2003, about 85 000 large rainbow trout (800–3400 g) escaped from a fish farm close to Sagafjord in a storm. The latter fish are hereafter termed "adults", as they were scheduled to be processed within 6 months. Rainbow trout from both escape events were captured with floating gillnets (Rikardsen *et al.*, 2000) each month from June to August 2002 in Altafjord ($n = 43$ fish), and from March to May and July to August 2003 and again in May 2004 in Sagafjord ($n = 172$ fish; Tables 1 and 2). All sampled fish were measured (fork length, L_F) to the nearest mm and weighed (W) to the nearest g. On average, fish shrink about 3% during freezing (Rikardsen *et al.*, 2004a), so length was adjusted accordingly after thawing. The relationship between weight and length was estimated according to Fulton's condition factor $C = 100\,WL_F^{-3}$.

Table 1. Biological characteristics and marine diet of post-smolt rainbow trout in Altafjord during different months of 2002. The diet is expressed as frequency of occurrence (%) of different prey items and as prey abundance (percentage of the total stomach contents by weight) for the main prey groups (in parenthesis). Forage ratio (F_w) is given as weight of stomach/weight of fish × 100.

Parameter and prey	June	July	August
n	31	6	6
% Empty	13 (4)	0	0
F_w (±s.d.)	0.32 ± 0.37	1.59 ± 1.7	1.16 ± 0.98
Weight (±s.d.)	221 ± 46.6	251 ± 46.6	471 ± 79.5
Length (±s.d.)	261 ± 13.0	275 ± 25.3	331 ± 20.4
Condition factor (±s.d.)	1.23 ± 0.15	1.16 ± 0.13	1.29 ± 0.16
Relative lipid level	6.9 ± 1.6	6.1 ± 2.0	5.4 ± 2.0
Prey			
Gastropoda	4 (0.2)		
Crustacea	74 (31.7)	4 (1.3)	0
Amphipoda sp.	59		
Idotea baltica	4		
Thysanoessa sp.			
Unidentified shrimp	4		
Unidentified crustacea	7	4	
Insecta	74 (48.4)	67 (24.0)	50 (37.5)
Adult	56	67	50
Larvae	37		
Pisces	15 (7.2)	83 (74.7)	75 (62.5)
Clupea harengus		17	75
Ammodytes spp.	15	67	50
Gadiodae	4		
Unidentified fish			25
Indigestible items	33 (12.5)	0	0
Algae	15		
Terrestrial vegetation	19		

Stomachs were removed from each fish, opened, and the prey identified. The forage ratio (F_w) was estimated from the ratio of the total wet mass of stomach contents (0.001 g) to the wet mass of the whole fish multiplied by a factor of 100 (empty stomachs included), and used as an index of feeding intensity between the rainbow trout in the two fjords, and between the different sampling periods. The importance of each prey category in the diet was expressed as prey abundance, i.e. the percentage a prey taxon constituted the total stomach contents (by weight) in all predators, and by frequency of occurrence, the percentage of fish in which a prey type occurred (empty stomachs excluded) (Amundsen *et al.*, 1996; Rikardsen *et al.*, 2003). Stomach contents of each fish were identified and classified into several prey groups, including "indigestible" contents (Tables 1 and 2).

Table 2. Biological characteristics and marine diet of adult rainbow trout in Sagafjord during different months of 2003 and 2004. The diet is expressed as frequency of occurrence (%) of different prey items and as prey abundance (percentage of the total stomach contents by weight) for the main prey groups (in parenthesis). Forage ratio (F_w) is given as weight of stomach/weight of fish × 100.

Parameter and prey	March 2003	April 2003	May 2003	July 2003	August 2003	May 2004
n	46	64	34	9	8	11
% Empty	39	6	6	11	13	0
F_w (±s.d.)	0.05 ± 0.06	0.43 ± 0.51	0.15 ± 0.11	0.28 ± 0.39	0.11 ± 0.17	0.77 ± 0.88
Weight (±s.d.)	1 751 ± 548	1 531 ± 493	1 912 ± 516	1 703 ± 585	1 612 ± 435	1 500 ± 602
Length (±s.d.)	470 ± 33	442 ± 44	488 ± 36	500 ± 52	490 ± 49	526 ± 50
Condition factor (±s.d.)	1.64 ± 0.22	1.72 ± 0.22	1.59 ± 0.20	1.33 ± 0.17	1.20 ± 0.17	1.00 ± 0.19
Relative lipid level	—	9.75 ± 0.46	—	6.50 ± 1.60	6.29 ± 1.39	2.82 ± 0.60
Prey						
Mollusca	14 (6.6)	8 (1.4)	6 (0.8)	25 (0.7)		27 (2.6)
Gastropoda	7	7		13		9
Bivalvia	7	2	6	13		18
Polychaeta	4 (1.1)	2 (0.7)				9 (0.1)
Crustacea	7 (1.4)	48 (21.1)	38 (2.3)	25 (2.1)	14 (0.3)	82 (16.6)
Copepoda sp.		3				
Amphipoda spp.	7	16	19	13	14	64
Idotea baltica		2	13			
Thysanoessa sp.		22	13			
Unidentified shrimp		10		13		
Hermit crab	4	2				
Cirripeda sp.						36
Echinodermata	14 (1.6)		6 (7.2)			
Sea urchin			6			
Sea star	14					
Insecta				75 (6.3)	86 (37.3)	45 (0.8)
Adult				75	86	
Larvae						
Pisces		10 (0.3)		75 (83.3)		36 (4.9)
Clupea harengus				25		
Ammodytes spp.				50		
Gadiodae						
Gobiidae						36
Unidentified fish		10		38		
Indigestible items	93 (89.3)	90 (77.0)	90 (90.1)	38 (7.5)	100 (62.4)	100 (75.0)
Algae	93	90	88	38	100	100
Terrestrial vegetation	29	7	6		14	45
Stone		3				27
Plastic			6			
Paper		3				
Bird feather		3		13	14	18

A relative estimate of mesenteric lipid (fat) content was used to supplement the condition factor as an indication of the energy content of the fish, because condition factor alone is not necessarily a consistent indicator of the lipid content of the fish (Rikardsen and Johansen, 2003). The mesenteric lipid content was scored from 1 to 10, where 1−3 represented different grades of low lipid content, 4−6 medium lipid content, 7−9 high lipid content, and a grade of 10 represented a very high level of lipid (where the fat tissue almost completely covers the internal organs). Although subjective, this method correlates significantly ($r^2 = 0.73$) with the actual lipid content of salmonids (Rikardsen *et al.*, 2002). For consistency, all estimates in the present study were carried out by the same person, and therefore should be comparable on a relative basis when comparisons are made between fjords and sampling periods.

Results

Post-smolt (120–340 g, age 1+) and adult (800–3400 g, age 2+) rainbow trout had different feeding patterns after escaping from the two fish farms in northern Norway (Tables 1 and 2, Figure 1). Post-smolts fed actively on marine prey and increased their forage ratio from 0.32 in June (first month after escape) to >1 by July and August (Table 1, Figure 1). Only 13% of the post-smolt stomachs were empty in June, whereas all had been feeding during the next 2 months (but note that just six fish were captured in each of June and July). In contrast, escaped adult fish had a very low forage ratio during the first 6 months of sampling (March–August; $F_w = 0.05-0.43$), but the ratio increased some 15 months after escape (May; $F_w = 0.77$; Table 2, Figure 1). The percentage of empty stomachs was highest in March (39%) and varied between 0% and 20% during the rest of the sampling period.

Insects and crustaceans were consumed by 74% of the post-smolts sampled during the first month after escape (June) and collectively represented 80% of the diet by weight (Table 1). Only 15% of the post-smolt fed on other fish during the same period (June). This increased to more than 75% for the fish sampled in July and August, representing 75% and 63%, respectively, of the diet in terms of weight. Indigestible items were only found in the post-smolt stomachs during the first month after escape, accounting for 13% of the total weight of contents.

In contrast, indigestible prey items were taken by 90–100% of adult escaped fish, and represented 62–90% of the total contents by weight. The only exception was in July, where indigestible prey accounted for 8% and fish larvae as much as 83% of the diet, although with a corresponding forage ratio of just 0.28 (Table 2). Insects were taken by more than 75% of adult fish in July and August, representing 6% and 37% of the diet by weight, respectively. Indigestible items consumed were primarily portions of seaweed (*Fucus* spp.) and small pieces of wood or terrestrial vegetation, but also included such items as small stones and pieces of plastic or paper. However, although contributing little to their overall diet, the variety of marine items preyed upon by adult fish was relatively high and included different species of crustaceans, polychaetes, molluscs, and echinoderms (Table 2).

There was no significant change in condition factor of post-smolts during the sampling period (t-test, $p = 0.30-0.38$), whereas the relative lipid content decreased significantly during the same period (t-test, $p < 0.001$, Table 1). In contrast, there were significant declines in both condition factor (from 1.7 to 1.0) and relative lipid content (9.8–2.8; t-tests, $p < 0.001$, Table 2) in escaped adult rainbow trout over the period extending from April

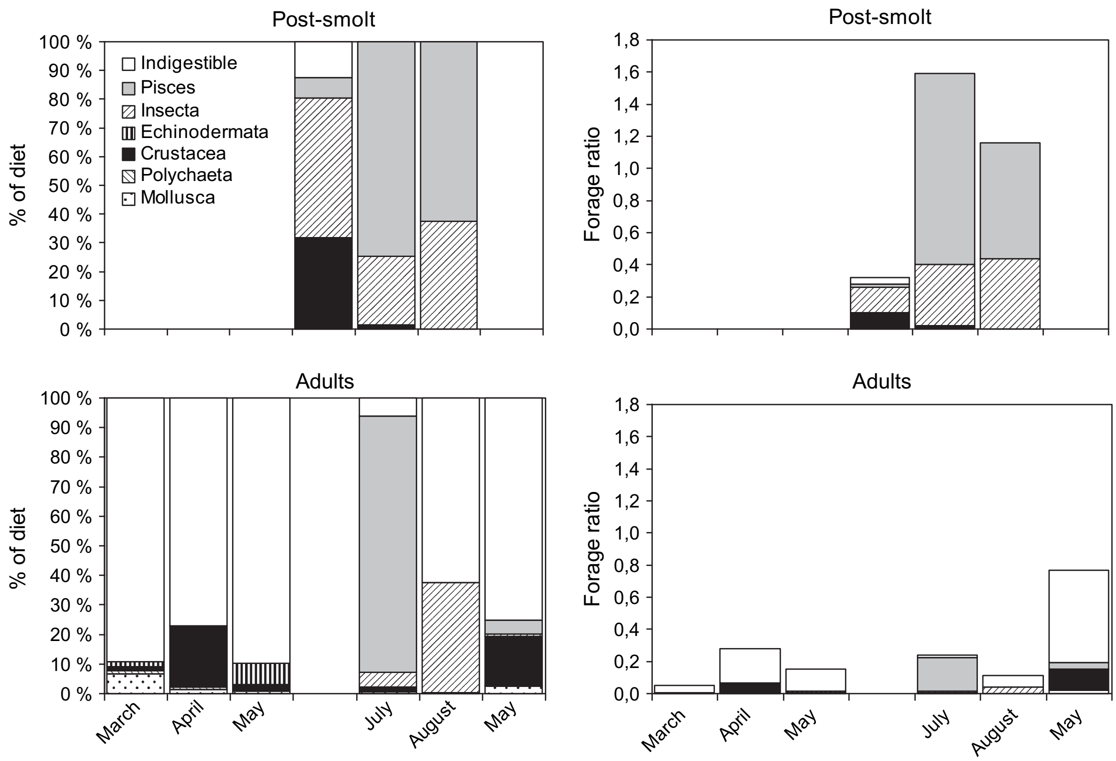

Figure 1. Prey abundance of escaped post-smolt (upper) and adult (lower) rainbow trout expressed as a percentage of total number of prey groups (left) and as forage ratios of the different prey groups (right).

(second month after escape) until May the next year (fifteenth month after escape). While the average size of post-smolts increased during the sampling period (t-test, $p < 0.001$), there was no consistent change in size of the escaped adult fish (Tables 1 and 2).

Discussion

Hatchery rainbow trout at post-smolt and adult stages adapted differently to natural marine prey after escaping from two fish farms in northern Norway. Post-smolts readily adapted to natural marine prey, and 1 month after escaping had a forage ratio similar to values observed for other wild anadromous species in northern Norway, including Arctic charr *Salvelinus alpinus* (L.), sea trout *Salmo trutta* L., and Atlantic salmon (Rikardsen *et al.*, 2000, 2002, 2004a, 2006; Rikardsen and Amundsen, 2005). Further, sea trout of similar size captured in the same gillnets as the rainbow trout had only slightly higher forage ratios (1.50−1.99) than the escaped rainbow trout (1.14−1.59) in July and August, but the ratios were about twice as high (0.70) as the rainbow trout values (0.38) in June (A. H. Rikardsen *et al.*, unpublished data). Arctic charr captured in the same nets in July had somewhat lower forage ratios (1.27) than both rainbow trout and sea trout. Collectively, the results indicated that escaped post-smolt rainbow trout can readily adapt to feeding on natural marine prey with similar feeding intensities as other wild anadromous salmonids within the same general area.

The composition of the diet of escaped post-smolts consisted mostly of fish larvae, particularly sand lance *Ammodytes* spp. and herring *Clupea harengus*, together with some insects and crustaceans. Those items are also among the most frequently taken marine prey of other native anadromous species in northern Norway (Grønvik and Klemetsen, 1987; Rikardsen *et al.*, 2000, 2002, 2004a, 2006; Rikardsen and Amundsen, 2005), illustrating similar foraging preferences between the two groups of fish. Rainbow trout are thought to be potential competitors of native salmonid species in European watercourses (Hindar *et al.*, 1996; Landergren, 1999). Moreover, in some New Zealand streams, introduced spring-spawning rainbow trout were a potential source of mortality to introduced brown trout owing to redd superimposition (Scott and Irvine, 2000). Hence, concern continues to be expressed about the potential impacts of escaped farmed fish on wild populations (e.g. Skilbrei *et al.*, 2003), including escaped rainbow trout, because this may also be the case in Norway if rainbow trout establish persistent local populations.

The increase in average size and the stable condition factor of post-smolts during summer indicates that these fish are quite capable of feeding and growing at sea following escapement. The increase in average size was largest from July to August, when fish also had the highest forage ratios. The reduction in lipid content during the same period may be related to the change from high energetic pellets to less fatty live prey combined, possibly, with the increase in activity level associated with searching for live prey. If this assumption is correct, fish may direct more of their energy surplus achieved through foraging into protein growth rather than into lipid storage, resulting in increased weight but reduced overall fat content (Jobling, 1994; Rikardsen and Elliott, 2000).

In contrast with post-smolts, no increase in size was observed for the escaped adult rainbow trout. Rather, there was a clear reduction of both condition factor and relative lipid content during the sampling period. Those fish had consistently low forage ratios and were feeding primarily on indigestible items such as algae (mostly the vesicles of seaweed, *Fucus* spp.) and terrestrial vegetation (pieces of wood and leaves). Although they fed proportionally more on fish larvae and insects 5−6 months after escape (July), their forage ratios remained low. However, although generally contributing little to their diet, a great variety of marine prey was taken, including polychaetes, echinoderms, molluscs, and several crustaceans. Prey such as gastropods, bivalves, hermit crabs, barnacles, and echinoderms are seldom reported in diet studies of other wild anadromous salmonids (Grønvik and Klemetsen, 1987; Rikardsen *et al.*, 2000, 2004a, 2006; Dempson *et al.*, 2002; Klemetsen *et al.*, 2003; Rikardsen and Amundsen, 2005). It is possible that some indigestible items, especially the vesicles of seaweed, wood pieces, and stones, are consumed by adult fish because of the similarity of their shape to the artificial pellets they had been accustomed to eating. This may in part be due to the longer time adult rainbow trout spent in caged captivity before escape than post-smolts did. This may partially explain why escaped adult fish appear to have greater problems adapting to marine prey after escape.

In conclusion, results from this study indicate that adaptation to marine prey by escaped hatchery rainbow trout depends on fish size and age at release, those escaping at an earlier or younger stage being better able to adapt to marine prey. Consequently, these fish are likely to attain energy levels sufficient for their subsequent survival and, possibly, successful spawning and colonization of local streams.

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