Taonga and mahinga kai of the Te Arawa lakes: a review of current knowledge - Smelt

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1. Introduction

The common smelt is indigenous to New Zealand and like the kōaro, it is fundamentally a diadromous species found primarily in rivers. However, it also forms landlocked lacustrine populations. Larval and juvenile smelt can be confused with kōaro because of their similar body shape and lack of pigmentation. However, smelt are readily distinguished from kōaro by the presence of scales and an adipose fin (Figure 1). They also have a characteristic ‘cucumber’ smell (McDowall et al. 1993). A comprehensive review of the common smelt was carried out by Ward et al. (2005), but this covered both lacustrine and diadromous populations and so did not deal with lacustrine populations in the Te Arawa lakes in detail. This review focuses on what is known about the life history and habitats of lacustrine smelt in the Te Arawa lakes.

Figure 1: Adult smelt showing scales and the small adipose fin (circled) between the main dorsal and caudal (tail) fin (photo courtesy of S. Moore, Landcare Ltd).

The origin of smelt in Lake Rotorua and Rotoiti (but not other lakes) has been queried. Strickland (1993) put forward the proposition that smelt were stocked into the Te Arawa lakes by Māori and were present there in pre-European times. There can be no doubt that smelt were stocked into the lakes. They are not capable of ascending even small falls or rapids and are generally confined to the lower reaches of rivers. They will not have reached the Te Arawa lakes naturally and can only have been stocked into them by humans. Strickland (1993) proposed that early Māori stocked Lake Rotorua with smelt (as well as kōaro) and that both coexisted. In contrast, Burstall (1980) proposed that smelt were introduced as a food for trout by early European settlers.

Strickland’s (1993) proposition is at odds with the historic accounts of the species of fish present in the Te Arawa lakes in pre-European times, none of which refer to or identify smelt as being present. For example, Stafford (1986) reviewed the history of the Te Arawa lakes prior to 1900, and stated that at this time 'inanga' and 'kōkopu' were the juvenile and adult stage of kōaro, respectively, and that the lakes contained this species and the toitoi along with a few (stocked) eels. Furthermore, in recent evidence provided to the Waitangi Fisheries Commission on the Te Arawa lakes, 'inanga' was used by Māori to refer to the juvenile stage of kōaro, whereas 'kōkopu' referred to the adult stage of this species (Habib, 2001). There is no mention of smelt. It is also very difficult, notwithstanding Māori knowledge and skill of fish stocking, to accept that the early Māori settlers had the ability to bring smelt to these lakes from the coast. Smelt are extremely difficult to keep alive over long distances, even with modern technology. Furthermore, if they had been successfully introduced to Lake Rotorua, they would surely have been transported to other nearby lakes and this did not happen. Jolly (1967) reported the results of Department of Internal Affairs surveys carried out in 1931-1932 after Lake Rotorua was stocked with smelt. These showed that smelt were present in lakes Rotorua, Rotoiti, Rotoehu and Ōkataina at this time, but not in lakes Tarawera, Ōkareka, Rotokākahi, Tikitapu, and Rotomāhana.

In contrast, Burstall's (1980) account of the stocking of smelt into Lake Rotorua accords with the first records of this species being found in Lake Rotorua (Phillipps, 1924b & 1926). A detailed account of the attempts and eventual success of smelt stocking in Lake Rotorua in the 1920s is provided by Burstall (1980), and McDowall (1990a) expands on this. After smelt were successfully established in Lake Rotorua and Rotoiti in the early 1920s, they were subsequently spread to all other Te Arawa lakes. Smelt were present in lakes Rotorua, Rotoiti, Rotoehu and Ōkataina by 1930 (Jolly, 1967). Liberations of smelt were then made into lakes Tarawera, Rotomā, Rerewhakaaitu, Ngāpouri and Ōkaro in 1932 (McDowall, 1990a). It can be assumed that Lakes Tikitapu, Ōkareka, Rotomāhana, Rotokawau, and Ngahewa were also stocked after this as these lakes now all contain populations of smelt (Smith, 1959). Smelt were then introduced to lakes Taupō in 1934 and to Waikaremoana in 1949 (McDowall, 1990a). However, they were not introduced to lakes Rotopounamu, Rotoaira or Waikareiti. Although Rotopounamu was later (illegally) stocked sometime between 1981 and 1991 (Rowe, 1993b), smelt do not occur in lakes Rotoaira or Waikareiti today. (NB. The kōaro is still relatively common, if not abundant, in both these lakes, despite rainbow trout being present for over a century).

2. Common smelt in the Te Arawa lakes - past and present

Schools of smelt (of all size classes) are periodically harvested by members of Te hapū o Ngāti Pikiao as they move up the Ohau Channel from Lake Rotoiti to Rotorua (Kusabs, 1989). Large quantities of smelt were harvested from this fishery prior to the installation of the control weir in the early 1990's. Up to 30 whānau would use whitebait traps (elongated cylindrical nets) to harvest smelt from about October to February and juvenile smelt from December to April. The nets are fished passively relying on the upstream movement of smelt, while the active scoop netting method commonly practices in the whitebait fished is generally discouraged (Donald, 1996).

The smelt fishery has reputedly been affected by the construction of this weir which is used to maintain the level of Lake Rotorua. However, the decline in smelt numbers in Lake Rotoiti related to its increased trophic status (Rowe et al. 2006) may also have contributed to the decline of this fishery. The proposed diversion wall (Rowe, 2005) can be expected to reduce this fishery further, unless a fish pass can be created for smelt, and monitoring is currently being carried out to determine the pattern and extent of smelt movements in this channel.

Common smelt were occasionally harvested from the sandy beaches of the Te Arawa lakes (particularly lakes Rotoiti and Rotorua) using seine nets (known locally as scrim nets). Adult smelt were targeted in the spring when they were congregating to spawn. This method was used up until the 1970's but was discouraged by the Department of Internal Affairs - the fishery managers at the time. This harvesting method is no longer practiced but there is some interest in reviving the method given the decline in catches from the Ohau Channel (Ngāti Pikiao hui, 2006).

3. Role of smelt in fisheries

The successful establishment of smelt in the Te Arawa lakes (as well as in Taupō) helped to stabilise the rainbow trout fisheries in these lakes (Hobbs, 1948; Burstall, 1980; McDowall, 1990b; Rowe et al. 2002c). Smelt soon became the major prey species for trout in most of the large clear lakes, and an important supplementary prey in the smaller, more turbid lakes (Smith, 1959; Rowe, 1984). However, the successful introduction of smelt was at the cost of kōaro. Although the kōaro fishery had already collapsed by the time smelt were introduced, the introduction of smelt is likely to have lead to the virtual extinction of kōaro in some of the shallow lakes (e.g., Rotorua, Rotoehu), and caused a further decline in kōaro abundance in the deeper lakes (e.g., Rotoiti, Ōkataina, Tarawera, Ōkareka).

In the Ohau Channel between lakes Rotoiti and Rotorua, the large runs of kōaro that would once have occurred were replaced by large runs of migrant smelt. These formed the basis for a new Māori fishery in the channel to replace that provided by juvenile kōaro. Although Ngāti Tūwharetoa occasionally harvest smelt from the shores of Lake Taupō using seine nets, this is not practiced in the Te Arawa lakes.

4. Life history, distribution, movement and habitat

As with the kōaro, the smelt is a diadromous species in rivers, but readily forms land-locked populations in lakes. However, the life history of smelt in lakes is relatively short compared with that of kōaro. The smelt is a semelparous species, which means that most adults die after spawning at an age of 1+. Stephens (1984) indicated that some smelt, having spawned in spring, could spawn again 6-8 weeks later. It is not known whether these fish grow another gonad or are partial spawners (i.e., they release some but not all eggs on each spawning occasion). Hence, smelt may spawn several times per season, but do not spawn over two seasons. The smelt's strategy for reproduction relies on the production of a large number of eggs by one age cohort each year. This contrasts with iteroparous species (e.g., kōaro) which rely on the production of eggs by multiple age cohorts each year over a number of years.

The spawning of smelt in central North Island lakes has been studied by Jolly (1967) and Stephens (1984) and summarised by Ward et al. (2005). The main spawning season is in spring (starting in September), but in Lake Taupō, spawning occurs sporadically over summer and extends into March. Both Stephens (1984) and Jolly (1967) found eggs on shallow (0.5-2.5 m), sandy beaches. However, Stephens (1984) failed to find any on stony or weedy shores in Lake Taupō, and Jolly (undated) found none in muddy or silty waters, nor on rocky shores. The preferred spawning substrate is therefore clean sand in shallow (0.5-2.5 m deep) water. This does not mean that spawning cannot occur if sandy substrates are absent: just that smelt prefer to lay their eggs on shallow, sandy shores because this presumably maximises egg survival. Smelt also spawn on sandy substrates in the slowly-moving or slack water of inlet streams. In Lake Taupō, where there are a number of major rivers and streams, recruitment of larvae from stream spawning is thought to be significant, especially in years when strong gales and wave action prevent spawning on the eastern shores (pers. comm. Dr M. Dedual, Department of Conservation). Stream spawning also occurs in many of the inlet streams of the Te Arawa lakes, however, adult smelt are not as common in the colder, spring-fed streams (e.g., Awahou, Waititi, Hamurana, Ngongotaha) as in the warmer, catchment fed streams (e.g., Utuhina).

The time required for egg incubation decreases with water temperature (Mora and Boubée, 1993; Hannus, 1998) and can be relatively short. Mora and Boubée (1993) indicated that the optimal temperature for the incubation of eggs of riverine smelt was 14-18ºC. At 18ºC, incubation times ranged from 10-18 days (Mora and Boubée, 1993; Hannus, 1998). However, shorter times may be possible for lacustrine smelt. Jolly (1967) found that eggs for Lake Rotorua smelt hatched after about 8-10 days at room temperature.

After hatching, the larvae are about 4 mm long and planktonic. They are quickly dispersed throughout the water column and spread throughout the lake. Larvae occurred mainly in the open waters of lakes Rotorua and Rotoiti at depths ranging from 0-40 m (Rowe, 1993a). High densities occurred at some depths, but not at others, and there was no discernable pattern in the depth distribution of larval smelt. Larvae range in size from 4-30 mm and have no air bladder. This contrasts with the smaller larval bullies that also occur in the open waters of the Te Arawa lakes. Larval bullies have an air bladder and so are detectable by high frequency echosounder (Rowe, 1993a). They also have a much more restricted depth distribution than larval smelt.

Once smelt exceed a size of about 25 mm long, they become pigmented and surface orientated. Like the juvenile kōaro, they aggregate into schools near the lake surface where they feed primarily on zooplankton. At this stage/size, they are a major prey for the rainbow trout. In clear lakes, schools of juvenile smelt occur from the lake surface down to about 20 m, but in turbid lakes they have a much shallower and narrower depth distribution (Rowe and Taumoepeau, 2004). This may be related to the reduced light penetration in turbid lakes. However, it may also be a function of food availability and/or reduced risk from predators in more turbid waters.

Once smelt are around 30 mm long, their diadromous origin reasserts itself and they become migratory, moving shorewards and entering small inlet streams, just as their marine counterparts move into rivers as schools of whitebait. Particularly large runs of smelt occur in the Ohau Channel from Rotoiti into Lake Rotorua (Jolly, 1967; Mitchell, 1989a; Donald, 1996). This is thought to result in a loss of smelt from Rotoiti to Rotorua (Jolly, 1967), but the extent of this movement is difficult to measure and may be partly compensated for by passive drift of larval smelt from Lake Rotorua down the Ohau Channel and into Lake Rotoiti (Rowe, 2005).

Adult smelt (>50 mm) are also schooling and, during the day, they occupy deeper waters than the juveniles (Rowe, 1994). In near pristine lakes such as Rotomā and Ōkataina, where the water is relatively clear and where the summer depth distributions of fish are not affected by hypolimnetic de-oxygenation, schools of adult, 50-70 mm long smelt occur in relatively deep waters (50-70 m). However, in Lake Rotoiti, such smelt occurred in shallower waters (20-60 m), and in late summer and autumn, when the hypolimnion was de-oxygenated, they were forced into even shallower waters (< 30 m deep) (Rowe, 1994). Acoustic studies of the distribution of adult smelt in shallow lakes (e.g., Lake Rotorua) show that they are usually found close to the lake bottom and generally in waters over 5 m deep (unpubl. data.). In Lake Ngāpouri (max. depth 26 m), hypolimnetic de-oxygenation occurs below 7 m in autumn, and all smelt are forced into the top 7 m of the lake at this time. This 'habitat squeeze' could increase predation on smelt by both shags and trout, although this may be mitigated somewhat by the more turbid conditions in this lake.

At night, the schools of adult smelt break up as individual fish move towards the lake surface (Rowe, 1993a). A return migration to deeper waters occurs just before dawn. The deep-water, daytime distribution of adult smelt is thought to reduce predation risk (from trout and shags) whereas the nocturnal migration to surface waters allows them to feed at night. However, feeding by smelt on zooplankton is likely to depend on vision and may occur during the day as well as at dusk and dawn. If so, the vertical migration may serve to expose smelt to warmer waters at night so that their physiological rates are increased and growth enhanced. The precise role of vertical migration in the life history of such fish is still to be determined.

Smelt are not distributed evenly throughout lakes, and a number of studies on their areal distribution in Lake Rotoiti indicate that they are more abundant in the deeper eastern basin than in the shallower western basin (Rowe et al. 2001a & b). Furthermore, within the eastern basin, some areas have consistently higher densities than others. The reasons for such differences in areal density are currently unknown, but have important implications for trout anglers, as the trout invariably concentrate around aggregations of smelt. The presence of discrete areas where smelt often concentrate in lakes also suggests that food supply may be consistently higher in such areas, or that the limnetic habitat is more favourable there. Such concentrations imply important fine-scale, hydrodynamic and production processes which are generally not incorporated into lake production models.

5. Prey species, predators and parasites

The diet of larval smelt has been studied in Lake Tarawera (Cryer, 1988). He found that smelt 20-30 mm long fed mainly on rotifers, particularly *Asplanchna* sp., rather than copepod or cladoceran zooplankton. In comparison, the larger (30-40 mm long), juvenile smelt fed more on copepods and cladocerans than rotifers. Similar results for juvenile smelt are reported by Jolly (1967) who found that copepods and cladocera were the main diet of smelt in the 30-50 mm long size range.

Larger smelt (> 50 mm long) feed on large zooplankton, such as cladocera, but also include a wide range of small insect larvae and invertebrates taken mainly from the lake edge or surface in their diet (Jolly, 1967; Boubée and Ward, 1997). For example, chironomid larvae and amphipods (*Paracorophium*), which are both found on the lake bed in shallow water, were important prey for large smelt at sites near Holden's Bay in Lake Rotorua (Jolly, 1967; Table 2).

Table 2: Prey species for 23 common smelt (43-68 mm long) seined at Holden's Bay, Lake Rotorua, in October 1976.

	Chironomidae			**Cladocera**	**Amphipods**	**Mites**
	larvae	pupae	Fly			
Frequency of occurrence	0.39	0.87	0.30	0.61	0.43	0.04
Mean no./fish	2.4	6.7	2	880.0	5.6	5.0

The inclusion of small benthic invertebrates in the diet of the larger smelt implies that they not only move towards shallow waters near the lake surface at night, but also move inshore to feed in the littoral zone. The largest smelt (>60 mm long) also feed on larval bullies (Jolly, 1967; Stephens, 1984; Forsyth and James, 1988) but not on larval smelt, which unlike bullies, are not concentrated within discrete depth layers (Rowe, 1993a).

Adult bullies have been reported to feed heavily on smelt eggs around lake margins (McDowall, 1990a), but there are no known predators of smelt larvae in the limnetic zone of lakes. Freshwater jellyfish (*Craspedacuspa sowerbyii*) occur in large numbers in the limnetic zones of the Te Arawa lakes in some years, but while they are known to feed on small larval fish, they are not known to be major predators of smelt or bully larvae.

The black and red-billed gulls (*Larus bulleri* and *L. scopulinus*) have several colonies around the edge of Lake Rotorua and they feed extensively on juvenile smelt, which they pick from the water surface (Gurr, 1975). Herons and kingfishers feed on smelt in inlet streams. Although smelt are undoubtedly an important component of these birds food resources, shags are probably more significant predators of smelt. Studies by Falla and Stokell (1945) and later Dickinson (1951) have indicated that both the pied shag and little black shags will feed on small fish including smelt in the Te Arawa lakes. Despite attempts to measure the extent of shag predation on trout, the extent of feeding on smelt has never been determined. However, there is good reason to expect that it is significant. Today, it is not uncommon to see large schools of small shags (500+ birds) 'working' schools of smelt around the edge of Lake Rotorua. The shags form a crescent-shaped line some 100 m wide on the lake surface. The birds at the rear of this line swim forwards while those at the front dive down to drive the smelt forward or feed on them and then re-emerge at the rear or side of the line. The whole flock thus moves forward over shallow parts of the lake, driving schools of smelt in front of it while individual shags feed on the aggregations of smelt below. The numbers of smelt taken by such flocks can be expected to be large, and with such foraging behaviour occurring several times a day every day, the resultant consumption of smelt would be high. Such foraging does not occur in deeper waters, and is confined to shallow areas where the schools of adult smelt cannot move into deeper water. At present, there is no quantitative data on smelt consumption by shags.

Although birds are significant predators of smelt, trout are the main predators in many of the Te Arawa lakes, especially the larger, clearer lakes (Smith, 1959; Rowe, 1984). Smelt are a major factor underpinning the faster growth rates of trout in these lakes (Rowe and Taumoepeau, 2004). Analyses of the size of smelt consumed by rainbow trout (Cryer, 1990; Stephens, 1984) indicates that predation is mainly on fish in the 30-50 mm size range. Some larger smelt (50-70 mm) are also taken but mainly in spring and summer when spawning occurs and these smelt are present on the shallow sandy beaches where they spawn and so are more vulnerable to trout.

Jolly (1967) listed black spot, glochidia, cestodes, and saprolegnia as the main parasitic infections of smelt in the Te Arawa lakes. Black spot is indicated by the presence of small black cysts under the skin of smelt. These are caused by the larvae of flukes. Glochidia are the juvenile forms of the freshwater mussel and attach to the fins of small fish such as smelt when they feed near the lake bed (McDowall, 2002). They hitch a ride on a smelt and fall off when it reaches suitable habitat for mussels in shallow water. The cestode worm was present in small cysts on the gut wall. *Saprolegnia* is a fungal infection which occurs on the fins of fish where an injury has occurred.

6. Age, growth fecundity, maturation and population structure

The first growth rate estimates for smelt in the Te Arawa lakes were provided by Phillipps (1926) from sequential samples caught in the Ohau Channel in 1919. He calculated a growth rate for juvenile fish (size range 35-65 mm) of just over 2 mm per month. Jolly (1967) also attempted to measure the growth rate and age of smelt in the Te Arawa lakes. Juvenile fish assumed to be about 12 months old and about 35 mm in length, were thought to grow by about 20 mm to reach a size of close to 50 mm over the following year (i.e., a growth rate of 1.7 mm per month). Thus, smelt of 50 mm length would be about 2 years old when they spawned. However, other smelt kept in ponds grew at a far faster rate than those in the lake and were 75 mm long after a year's growth. Later, the ages of riverine smelt from the Lower Waikato River were determined from daily growth rings in otoliths (Ward and Boubée, 1996). The results indicate a growth rate of around 80 mm per year (or 6.6 mm per month). This is much faster than the growth rate for lacustine smelt estimated by Jolly (1967) and Phillipps (1926), but lacustrine smelt may grow at a much slower rate than riverine smelt.

Jolly (1967) found that some smelt from Lake Rotorua were mature at a length of 43 mm, but most matured at a larger size and the mean length for mature smelt was 50 mm. Fecundity for smelt in the size range 40-60 mm was 800-1000 eggs.

Despite the uncertainty in growth rate estimation for lacustrine smelt, it is apparent that they can reproduce at a relatively early age and that few survive spawning. As a consequence, there are few smelt larger than 70 mm long in these lakes and none will be older than 3 years. The larger fish (50-70 mm) may well be the progeny of late (autumn) spawning smelt which over-winter in the lakes, growing to a larger size than the younger, spring-spawned fish that reach 50 mm and spawn as 0+ old fish. Alternatively, the smelt that do not spawn at the end of their first (0+) year may over-winter and contribute to the stock of large-sized 1+ smelt that spawn the following year.

Northcote (1988) studied variation in the number of gill rakers and vertebrae of juvenile smelt from the Te Arawa lakes and found small but significant differences between winter and summer samples of smelt from Lake Rotomā, but not Lake Tarawera. This difference may indicate the existence of spring versus autumn spawned stocks of smelt in Rotomā. Data from Lake Ngāpouri and Ōkaro implied that smelt spawned in spring in the former lake and autumn in the later, reinforcing the likelihood of spring and autumn spawning by smelt. However, these data were for one year and this seasonal difference may have been produced by seasonal variations in spawning success rather than by a lake-specific difference in spawning season. More interestingly, there was a significant and persistent difference in gill raker counts (but not vertebrae) for smelt from eutrophic versus other lakes. This difference (fewer gill rakers for smelt in eutrophic lakes) was independent of spawning season and may reflect an effect of eutrophication on smelt. However, it should be noted that similar measurements by McDowall (1979) revealed no such trend.

There is little information on sex ratios for smelt in lakes. Jolly (1967) found that males tended to be slightly larger than females and samples obtained by her were composed of 43-81% females. This suggests that females may slightly outnumber males.

7. Environmental tolerances

Smelt are very sensitive to changes in their physical environment and are one of the more sensitive of the native fish species in New Zealand. Their haematological profile means that they are particularly sensitive to stress from capture and handling (Neilson, 1996). For this reason they are a good theoretical species for setting environmental tolerances for fish (i.e., if smelt will survive, so will all other fish), but are not a practical fish for this purpose as they are so difficult to handle.

Temperature tolerances of eggs were determined by Mora and Boubée (1993) and for adults by Richardson et al. (1994). Although the temperature range for egg development was wide (10-25ºC), egg development was best at temperatures between 14-18ºC. Adult smelt had a temperature preference close to 16ºC. These data indicate that smelt require cooler water than many other native fish species. However, using field data on smelt distribution, Leathwick et al. (2005) predicted that smelt would occupy waters with a mean temperature of 19ºC in mid-summer. Although smelt prefer temperatures in the 16-19ºC range, they are a stenothermal species (Leathwick et al. 2005) and therefore likely to be more sensitive to a change in temperature than other fish species. It should be noted that the temperature preference data are for diadromous smelt and lacustrine smelt may have slightly different temperature tolerances.

Smelt prefer slightly alkaline waters with a pH of 8.2 (pH range 8-9) and avoided both acidic waters (pH <7) and highly alkaline waters (pH >9.5) (West et al. 1996). In general, the pH of inland lakes is alkaline (pH >7) unless there is a large inflow of acid water from geothermal sources, or from tannin-stained streams arising in either peaty swamplands or small streams beneath dense forest. Some of the Te Arawa lakes have geothermal inflows, but these are not sufficient to greatly influence the acidity of lake water. McColl (1972) measured the water quality in a number of the Te Arawa lakes and found that the pH generally ranged from 7-9 (i.e., alkaline waters). Only in Lake

Tikitapu was the water slightly acidic (pH range 6-7) and therefore less suitable for smelt.

Dean and Richardson (1999) measured the lethal oxygen concentration for smelt at 15 ºC and found that 50% mortality occurred at 1 mg/l after 36-42 minutes depending on whether fish were juveniles or adults. There was no mortality for either juvenile or adults at 3 mg/l oxygen. These findings accord with field observations of smelt distribution in the Te Arawa lakes. Adults are affected by low oxygen levels in the hypolimnion of lakes and are forced into shallow waters when these drop during summer. Smelt tolerate oxygen levels down to 2.5 mg/l, as do trout, but they do not occur below this level (Rowe, 1994, Rowe and Chisnall, 1995). Lakes in which hypolimnetic de-oxygenation currently limits the summer/autumn depth distribution of smelt include Ōkaro, Ngāpouri and Rotoiti. Smelt distribution is also affected in shallow lakes lacking a stable hypolimnion (e.g., Rotorua and Rotoehu), but only for brief periods during calm weather in summer and autumn.

Smelt are not particularly strong swimmers and have a limited upstream penetration of streams compared with many other New Zealand native fish. Nevertheless, they move into the inlet streams of lakes during summer months and are able to swim up the Ohau Channel from Rotoiti to Rotorua. Mitchell (1989b) indicated that they can sustain normal swimming when water velocities are less than 0.2 m/s, but rely on 'burst' swimming at maximum speeds when water velocities are at or over 0.5 m/s. As water velocities in streams often exceed 0.2 m/s, smelt are forced to move upstream close to the bank where the velocities are generally lower than in the centre of the channel. Where water velocities exceed 0.5 m/s (e.g., some places in the Ohau Channel), smelt are forced to swim at maximum speed, and upstream movement may be limited at such locations. In particular, the weir on the Ohau Channel now acts as a localised velocity barrier, creating a migration bottleneck with schools of smelt sometimes accumulating behind it (Mitchell, 1989a; Kusabs, 1989; Donald, 1996).

Increased turbidity does not appear to affect smelt directly. Feeding rates are not reduced by turbidities up to 160 NTU (Rowe and Dean, 1998; Rowe et al 2002b), but smelt have a shallower distribution in more turbid lakes (Rowe and Taumoepeau, 2004). This may be because of the protection from predation afforded by more turbid waters, or because the prey of smelt are in shallower waters in more turbid lakes. Although turbidity *per se* does not appear to affect smelt in lakes, the settling of silt, which is often responsible for increased turbidity, does. The suspended solids responsible for increased turbidity in lakes are thought to reduce spawning habitat for smelt by smothering sandy substrates with a layer of fine silt (Rowe and Taumoepeau, 2004). This either prevents smelt from spawning or results in increased egg mortality where spawning does occur.

8. Factors affecting population size

The relative abundance of smelt varies within the Te Arawa lakes, with smelt being more abundant in the clearer lakes than in the more productive, turbid ones (Peterson, 1982; Rowe and Taumoepeau, 2004). Smelt recruitment has been shown to be reduced in the more productive, turbid lakes in the Rotorua district compared with the clear, less productive lakes (Rowe and Taumoepeau, 2004). This decline in smelt recruitment contrasts with the increased recruitment of common bullies in such lakes. The extent of trout predation on smelt can be used as an indirect sampling tool and Rowe (1984) used this to show that adult smelt were less frequently consumed by trout in the more productive lakes compared with the less productive ones. Data on adult bully abundance showed the opposite trend (Rowe, 1999b). Although field data on adult smelt abundance in the Te Arawa lakes are limited (Peterson, 1982), they nevertheless support the suspected lower smelt abundance in the more productive lakes.

Confirmation that an increase in lake productivity results in a decline in smelt abundance is required as this has major implications for the trout fisheries as well as for management of smelt and lake water quality. Conventional sampling techniques (e.g., seine and fyke netting) are not effective for smelt population estimation in these lakes because the catchability of smelt varies greatly with the weather (e.g., wind/wave action and cloud cover), the seasons, as well as with lake water conditions (e.g., temperature and turbidity). Mid-water trawling has been attempted and found wanting for daytime sampling, however, it may prove useful at night when smelt migrate to the surface waters of lakes and are likely to be more vulnerable to netting. Because of the lack of direct sampling methods for smelt population assessment, high frequency (200 kHz) echosounding was used to study their spatial distribution in the Te Arawa lakes (Rowe, 1993a & 1994). This has been successful and more sophisticated acoustic methods are now being developed for smelt population estimation (Rowe et al. 2001a & 2001b; Rowe, 2005).

The reduced recruitment of smelt in the more productive Te Arawa lakes has been attributed primarily to increased turbidity and the resultant siltation of sandy substrates, which degrades smelt spawning habitats on beaches (Rowe and Taumoepeau, 2004). However, egg predation from the increased abundance of bullies may be an important contributing factor. Increased lake productivity not only increases siltation of lake beds by organic particulates, but it also increases both hypolimnetic de-oxygenation and the incidence of blue-green algae blooms. Hypolimnetic de-oxygenation, coupled with increased turbidity from high densities of planktonic algae, has been shown to reduce depth habitat for smelt in lakes (Rowe &

Taumoepeau 2004). Increases in the trophic status of lakes therefore affect smelt in several ways, but the most important is likely to be a reduction in recruitment caused by high egg mortality.

Large movements (migrations) of smelt between lakes also have the potential to affect the relative abundance of smelt. Jolly (1967) was aware that large annual summer migrations of smelt occurred from Lake Rotoiti into Lake Rotorua (via the Ohau Channel). She noted that no return migration had been observed and speculated that the smelt population in Rotorua was augmented by the immigrants from Rotoiti. If so, the converse also applies, and Lake Rotoiti will experience an annual loss of smelt. Some field evidence supporting this view is provided by acoustic data on smelt distribution and abundance in both lakes. For example, acoustic studies have revealed a large increase in the number of schools of juvenile smelt in the surface waters of Lake Rotorua during spring and early summer (unpublished data). Similarly, acoustic transects covering the whole of Lake Rotoiti have revealed a persistent reduction in the abundance of smelt in the western versus eastern end of this lake (Rowe et al. 2001a; 2001b; 2006). Furthermore, acoustic surveys carried out over short time intervals (i.e., days to weeks) revealed a shift in smelt abundance from east to west in lake Rotoiti.

Such large migrations of smelt are not known between other hydrologically connected lakes (e.g., Tarawera to Rotokākahi, Ōkareka to Tarawera, Ōkaro to Rotomāhana, or Ngāpouri to Tutaeinanga), probably because the connecting streams are much smaller and/or contain barriers to smelt upstream movements. Nevertheless, some smelt can be expected to enter these other lake outlet streams during summer months, but will return to the lake after spawning and/or if they reach an impassable barrier.

The planktonic food supply for smelt in the Te Arawa lakes may also prove limiting at times, and an understanding of the factors affecting this relationship could prove very useful for future lake and fishery management. Preliminary data on the feeding rates and nutritional status of smelt in several Te Arawa lakes were presented in Rowe (1997) and contrasted with those in Lake Taupō following the ash shower from the Ruapehu eruptions. Although this ash may have temporarily reduced smelt feeding and lipid levels in Lake Taupō smelt (Rowe, 1997), it resulted in a change in the dominant algal species (from diatoms to green algae) in the lake during the following spring (pers. comm. M. Gibbs, NIWA). This was followed by a larger than expected crop of large trout. Similar relationships between algal dominance and trout production have been noted in the Te Arawa lakes (pers. comm. R. Pitkethley, Fish and Game) and no doubt reflect an improved limnetic food chain leading to trout, via smelt.

9. Protection and restoration issues and options

Conservation and enhancement of smelt spawning habitats will be required to maintain both the smelt and trout fisheries in the Te Arawa lakes. Degradation of spawning habitats is thought to be caused mainly by an increase in lake trophic status. A reduction or halt in the trophic status of lakes through better nutrient control is therefore clearly the best long term solution for both species. However, in the short term, habitat improvement by silt removal from sandy beaches in spring, or sand replenishment may be a worthwhile remediation measure. However, such options will require much finer-scale data on where and when smelt spawn, and the testing of remedial options to identify their efficacy and cost.

Factors other than increased trophic status may also impact on smelt spawning habitats in lakes. For example, ski-lanes are often sited in the middle of clean sandy, shallow beaches around the lake and these beaches are intensively utilised over summer months by skiers. This use coincides with smelt spawning and may be inappropriate in some situations, due to the effects on eggs. There is clearly a need to identify where the major spawning grounds for smelt are in the Te Arawa lakes and when the smelt spawn on them. Such information will be needed to ensure better coordination between recreational use and fishery requirements.

Another factor that can be expected to affect smelt spawning habitat in lakes is lake level control (Rowe et al. 2002c). The maintenance of clean sandy beaches in lakes is dependent on wave action (i.e., on exposure to prevailing winds and on fetch). In exposed areas of shoreline, wind patterns will have the main influence on smelt spawning habitat. However, in sheltered areas or small lakes, the presence of clean sandy beaches is more dependent on seasonal lake level fluctuations which expose shorelines to desiccation and then re-inundate them, resulting in a clean sandy substrate. This natural cycle ensures that silt build up is minimised and more importantly, that macrophyte growth is restricted to deeper waters. When lake levels are controlled between very narrow limits (20 cm or less) macrophytes can be expected to invade shallow waters, reducing the inshore zone of sandy habitat.

The role of smelt in trout fishery maintenance in the Te Arawa lakes is well accepted. However, smelt may also play a potentially significant role in water quality control in some of these lakes through their planktivorous habits. Numerous studies have shown that zooplanktivorous fish can affect algal abundance in lakes by reducing the number of large, cladoceran zooplankton, primarily *Daphnia* (Carpenter et al. 1985; McQueen et al. 1986). Fish predation on zooplankton reduces their abundance to the point where they no longer exert control over algal populations. An increase in algal abundance then occurs, and in turn this results in a decrease in water clarity. Predator control of the planktivorous fish has been used to reverse this process and improve water clarity in some northern hemisphere lakes (Carpenter et al. 1985; McQueen et al. 1986). Unfortunately, the precise dynamics of this process are not well understood and it does not occur in all lakes or at all times. This issue aside, the existence of such a process begs the question ‘could smelt exert control over zooplankton in the Te Arawa lakes and hence influence water clarity?’ Such a process will be generally masked by the presence of trout which, as predators of smelt, can be expected to ensure that smelt densities are never high enough to exert control over the zooplankton. However, an artificial increase in the density of trout (and hence predation pressure on smelt) in Lake Ōkareka caused by deliberate over-stocking was associated with a marked increase in water transparency and increased occurrence of *Daphnia* (pers. comm. I Kusabs, 1994). Hence, smelt may well play a significant role in this lake’s limnology but this only becomes apparent when smelt density is strongly manipulated (Rowe and Graynoth, 2002). Although this possibility exists in theory, many factors influence the foodwebs of these lakes and a true appreciation of the role of smelt and trout in the lakes’ water quality will require much more fundamental research on food web dynamics (Rowe and Schallenberg, 2004).

A major threat to the smelt populations in the Te Arawa lakes could be posed by the introduction of exotic fish. The main species of concern is perch (*Perca fluviatilis*). Because it is a limnetic piscivore, it could be expected to impact heavily on the inshore populations of smelt, bullies and kōura. Predation by perch would be expected to reduce these species, especially in the more productive lakes. This would reduce the main prey species for trout and increase competition for food between perch and trout in the littoral zone. Although trout recruitment would not be directly affected, growth rates can be expected to decline.

10. Critical knowledge gaps

The priority information gap for smelt at present is knowledge of the location, size and use of beach spawning habitats. Spawning habitat is though to be the main physical bottleneck controlling smelt density in these lakes and knowledge of this is required to underpin management decisions on smelt conservation. However, important information on smelt population dynamics in the lakes is also lacking. For example, it is not known whether smelt numbers are limited in autumn by a reduction in planktonic food supply or by heavy trout and shag predation. Shags may play an important role in controlling smelt numbers in shallow lakes such as Rotorua, but not in the deeper lakes where smelt schools can evade predation by moving into deeper water during the day. Variations in year class strength related to either climate-related variations in spawning success and/or to variations in growth and mortality rates are also likely to have a large impact on smelt abundance and hence on the trout fisheries. Thus, the role of these factors in smelt population abundance also needs to be determined.

Finally, a method of accurately assessing smelt abundance is a fundamental management tool. It is required to identify the main factors affecting smelt abundance and to determine the success or not of any restoration measures. Acoustic methods are being developed for this (Rowe, 2005), but will require calibration.

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