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Natal fidelity: a literature review in relation to the management of the New Zealand hoki (*Macruronus novaezelandiae*) stocks

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EXECUTIVE SUMMARY

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A review of published literature on natal fidelity (a behaviour whereby a fish always returns to spawn on the spawning ground where it originated) is presented here. The aim of the review was to determine which species exhibit natal fidelity, and what methods were used to determine this characteristic. The likely applicability of any of the methods as a means to investigate natal fidelity in hoki was evaluated. Currently, two possible life history model structures for hoki are considered. One assumes natal fidelity; the other assumes that fish "choose" a spawning ground at random for their first spawning and always return to it in following years. If it was possible to demonstrate or refute natal fidelity in hoki then some uncertainty could be removed from the stock modelling process. However, a demonstration of natal fidelity requires the assignment of spawning individuals to their birth ground on the basis of distinguishable natal tags, or the tracking of individuals from fertilization to spawning. This is clearly a difficult challenge for any species.

It might be expected that natal fidelity is likely to occur more often in species with spawning areas that are enclosed geographically (i.e., freshwater, estuarine, or near-coastal species) than in dispersing, off-shore, pelagic species which may have more diffuse spawning areas. Some species, such as salmon or other anadromous fishes, are generally believed to exhibit natal fidelity. However, stray rates for these species can be high, and are variable over time. Proving natal fidelity for a significant proportion of adults in a marine species has rarely been achieved. The analysis of geochemical signatures in otolith cores, showing that these signatures can be linked to defined spawning areas, is the method that appears to have the most promise as a tool to determine natal fidelity in marine fishes. However, other methods (e.g., genetic analyses, and thermally-induced 'bar-coding' in otolith cores) have also proven useful.

Hoki is a problematic candidate for an investigation of natal fidelity. Because it has multiple spawning areas, all in relatively open locales subject to strong but variable current flows, the species is likely to experience relatively rapid and variable dispersal of eggs and larvae from the natal areas, reducing the effectiveness of any natural environmental tags. The relatively long spawning season adds further complication in this regard. However, because hoki are an off-shore species, widely dispersed in the non-spawning season, with multiple diffuse spawning areas, it is likely that any hoki population model assuming 100% natal fidelity is untenable. Even if natal fidelity is the preferred option for hoki from an evolutionary perspective, it is almost inconceivable that a large proportion of the population would not stray routinely. It appears that only one experimental method may be practical in any determination of the proportion of hoki exhibiting natal fidelity, i.e., the analysis of geochemical signatures in otolith cores. However, sample sizes would need to be large (to account for the multiple spawning areas) and comparisons involving numerous year classes would be necessary (to account for any between-year variations).

1. INTRODUCTION

Hoki (*Macruronus novaezelandiae*) is New Zealand's most productive finfish fishery. There are believed to be two separate sub-populations, based on the geographical separation of the two main spawning grounds (i.e., WCSI and Cook Strait), and on consistent morphometric and growth differences between adult hoki taken from the two main dispersed areas (Chatham Rise and Southern Plateau) and from the two spawning grounds (Livingston et al. 1992, Livingston & Schofield 1996, Horn & Sullivan 1996, Hicks et al. 2003). It is not known whether the differences between the two sub-populations are genetic, or if they are just the result of environmental differences between the Chatham Rise and Sub-Antarctic. No genetic differences have been detected with selectively neutral markers (Smith et al. 1981, 1996), although it is known that even a low exchange rate between stocks would reduce or remove genetic differentiation.

Small juvenile hoki from both spawning grounds migrate to the Chatham Rise off the east coast of the South Island and feed in this highly productive area for 3–4 years before maturing. Evidence suggests that fish that spawn on the west coast South Island head south to the Sub-Antarctic first, then on to the west coast South Island to spawn (and subsequently alternate between WCSI and the Sub-Antarctic), whereas those that spawn in Cook Strait go directly there from the Chatham Rise at about the same age (and subsequently alternate between Cook Strait and the Chatham Rise).

A situation where there are two sub-populations that are mixed during part of their life histories adds complications to the stock modelling process because it is not known if there are two completely separate stocks (i.e., fish spawned at a particular ground always return there to spawn), or if there is some transfer between the sub-populations (e.g., a fish spawned on one ground can subsequently spawn in a different area). Consequently, two life history model structures have previously been used for hoki assessments up to 2007 (Francis 2008). One assumes that fish always return to the spawning grounds where they began life (i.e., natal fidelity); the other assumes that fish "choose" a spawning ground at random for their first spawning (e.g., by following other adults), and return to that same spawning site in following years (i.e., adult fidelity). Since 2008, all hoki assessments have assumed that natal fidelity occurs (McKenzie 2011). If it was possible to demonstrate or refute natal fidelity in hoki then some uncertainty could be removed from the stock modelling process. Clearly, a fish that exhibits natal fidelity must also exhibit adult fidelity.

A cursory examination of the literature indicated that adult fidelity has been shown to occur for numerous marine fish species, primarily through tagging studies (e.g., Robichaud & Rose 2001, Hunter et al. 2003). However, comprehensive natal fidelity is much more difficult to demonstrate, though it is generally believed to occur in salmonids (e.g., Dittman & Quinn 1996, Quinn et al. 1999). Available information on hoki indicates that adult fidelity probably occurs; Smith et al. (2001) found significant differences in gill raker counts, and Hicks & Gilbert (2002) found significant differences in measurements of otolith rings, between samples of 3 year-old hoki from the 1997 year-class caught on the WCSI and in Cook Strait. However, when additional year-classes were sampled, differences in the mean number of gill rakers and otolith measurements between stocks were not always detected (Hicks et al. 2003), and, due to high variation, large sample sizes would be needed to detect these. The available information currently available on hoki allows no conclusions to be drawn on the likelihood of the species exhibiting natal fidelity.

The following review of the literature relating to investigations of natal fidelity (also known as philopatry) in fish species was conducted. It aimed to determine which species have been shown (or are claimed) to exhibit natal fidelity, or refuted to exhibit it, and which methods

were used, or could be used, to determine this characteristic. The likely applicability of any of the methods as a means to investigate philopatry in hoki was evaluated.

2. DEFINING 'NATAL FIDELITY'

The definition of natal fidelity is straightforward. A fish that exhibits this characteristic always returns to spawn on the spawning ground where it began life.

To demonstrate natal fidelity it is not sufficient to show that mature fish in the population always return to the same spawning ground year after year (this is adult fidelity), nor is it sufficient to show that juvenile fish found on or near a spawning ground always return to that ground to spawn after they mature. A comprehensive demonstration of philopatry requires the assignment of spawning individuals to their birth ground on the basis of distinguishable natal tags, or the tracking of individuals from fertilization to spawning (Bradbury & Laurel 2007). Clearly, obtaining direct measurements of connectivity at this level (i.e., between fertilised eggs and spawning adults) is a difficult challenge.

3. LITERATURE REVIEW

To follow a fish from birth to spawning maturity (and therefore prove or disprove natal fidelity) it is necessary to mark it in some way so that it can be identified at any later stage in its life. Marks, or tags, can be acquired naturally or artificially. The published literature specifically or potentially pertaining to natal fidelity is reviewed here for three species groups, i.e., freshwater and anadromous teleosts, elasmobranchs, and marine teleosts.

3.1 Freshwater and anadromous fishes

The phenomenon of 'homing' has been most extensively studied in the family Salmonidae (e.g., Dittman & Quinn 1996). Fry typically emerge from their natal stream gravel and immediately migrate downstream to a lake where they live for 1 or 2 years before smolting and migrating to sea. Salmonids exposed to natural or artificial odours during their transformation from freshwater resident parr to seaward migrating smolts will learn ("imprint") the odours and home to them at maturity (e.g., Scholz et al. 1976, Dittman et al. 1996). However, migration patterns indicate that home stream learning must occur before the sensitive period at parr-smolt transformation (Dittman et al. 1996).

3.1.1 Genetic methods

Genetic differentiation among subpopulations of sockeye salmon was investigated within nine intensively sampled lake systems located throughout the species range along the north Pacific coast (Varnavskaya et al. 1994). Allozyme allelic frequency data at nine highly polymorphic loci were used to examine genetic diversity among 163 samples collected from 68 distinct spawning sites and to identify subpopulation structure. Significant heterogeneity was detected among sites within all lakes. The greatest differentiation was evident among subpopulations exhibiting different spawning run timing or using different spawning habitats (tributary vs. littoral). These findings indicate that most sockeye home precisely to natal streams, not just to the lake where they smelted.

Olsen et al. (2003) examined microsatellite loci to genotype 32 putative Alaskan coho salmon populations from seven regions. Significant population differentiation was found within each

region, and the degree of differentiation among populations was large relative to that reported for other Pacific salmon species in Alaska. These results suggest that coho salmon populations are small and isolated relative to populations of other Pacific salmon, and the genetic diversity within and among coho salmon populations is influenced primarily by genetic drift, and not gene flow. Strong natal fidelity was indicated.

3.1.2 Environmental classification

Quinn et al. (1999) took advantage of the natural variation in otolith microstructure caused by differences in thermal regimes during incubation to test whether sockeye salmon homed to their incubation-emergence sites (rather than just to the lake where they reared before migrating to sea). Otoliths from adults that returned to discrete spawning areas in Iliamna Lake, Alaska, and Lake Washington, Washington, were classified based on comparison with otoliths from juveniles from the same sites that had experienced the same site-specific thermal regimes. Otoliths from four sites were classified in blind trials, based on increment patterns recorded in the region between the otolith's core and the onset of regular increment production following emergence (Quinn et al. 1999). Many salmonid otoliths display a "check" in the form of a very dark band or structural discontinuity that corresponds to the time of hatching. At emergence, a transition in increment appearance often occurs, in which broad or indistinct increments characteristic of the post-hatch alevin give way to the well-defined daily increments of the emergent fry (Volk et al. 1995). The analysis showed that the salmon were much more likely to return to their natal incubation site than would have occurred by chance, with estimated straying rates being less than 1% in four populations. However, other studies have shown that the prevalence of straying varies greatly among populations and among years, and any genetic or environmental factors that influence straying are not well understood (Quinn 1993).

Although Quinn et al. (1999) used thermal-induced marks in otoliths that had been naturally defined, it is possible, when rearing fry in a hatchery, to artificially induce a unique 'bar-code' pattern of daily otolith growth zones by subjecting the fry to a variable but unique regime of temperature changes. Thus, it is possible to mass-mark a batch of fish (Volk et al. 1990).

3.1.3 Meristics

Developmental markers, manifested as either meristic or morphological variation, have been used in studies of fisheries stock structure. This method may have some applicability in investigations of natal fidelity because fish larvae can show temperature-dependent effects on the development of meristic characters such as the number of vertebrae and fin rays and spines, as shown for chum salmon (Murray & Beacham 1988). Even differences in temperature history between spawning females can cause meristic differences in their progeny (e.g., Swain & Lindsey 1985). Consequently, if spawning grounds experience markedly different temperature regimes then meristic or morphological variation may result. However, no examples of investigations of natal fidelity using this technique were found in the literature.

3.1.4 Geochemical classification

Geochemical signatures in the otoliths of American shad (*Alosa sapidissima*) were analysed to determine natal origins and estimate rates of straying among river-specific populations along much of the Atlantic coast of USA (Walther et al. 2008). Elemental and isotopic ratios were obtained using laser ablation inductively coupled plasma mass spectrometry and isotope ratio mass spectrometry. Stable isotope ($\delta^{13}C$, $\delta^{18}O$ and $^{87}Sr:^{86}Sr$) and elemental (Mg:Ca, Mn:Ca, Sr:Ca and Ba:Ca) signatures in otoliths of juveniles varied significantly, allowing for an average of 91% cross-validated accuracy when classifying individual fish to their natal rivers. The ground-truthed geochemical signatures in the otoliths of juvenile shad were then

used to identify the natal origins of spawning adults in a single river system (the York River in Virginia). Approximately 6% of the spawning adults were strays from other rivers. The results suggested that although most shad spawning in the York River were homing to their natal river, there was much less fidelity to individual tributaries.

Walther et al. (2008) did find that the geochemical signatures in the otoliths of juvenile shad from two of the river systems differed significantly among years, primarily driven by fluctuations in $\delta^{18}O$ values. Otolith oxygen isotopes are deposited in equilibrium with the water they live in (Thorrold et al. 1997), so the variability was probably related to the source or amount of rainfall in the watersheds, or to fluctuations in mean annual water temperatures. The potential for $\delta^{18}O$ to be affected by various stochastic environmental effects highlights the importance of ground-truthing juvenile signatures from each cohort of interest when $\delta^{18}O$ is included in the classifying signature (and $\delta^{18}O$ was the most important classifying signature in this study). The second most important classifying signature was ^{87}Sr:^{86}Sr values, thus demonstrating the value of combining analyses of stable isotope ratios with elemental concentrations to obtain unique multivariate signatures in studies of this type. However, Kennedy et al. (2002) did show that the ^{87}Sr:^{86}Sr ratio alone was sufficient to establish the natal source (i.e., hatchery) of four returning Atlantic salmon.

Characterising the geochemical otolith core signature of juvenile rainbow smelt (*Osmerus mordax*) from different sites, then measuring the core composition of the adults from the same cohort later confirmed that the adults returned to their juvenile nursery grounds to spawn (Bradbury et al. 2008). Fish were sampled from six spawning locations in different estuaries, and otolith composition was examined using laser ablation inductively coupled plasma mass spectrometry. Single-element (i.e., Sr:Ca and Ba:Ca) and multivariate (i.e., discriminant function analysis) approaches both indicated estuarine residency predominated, with limited marine (0.7%) signatures indicative of rare marine movements. Multiyear spawning site fidelity was examined through a finclipping and visual implant elastomer experiment at each of the six locations. Annual spawning site fidelity ranged from 90 to 99%. It was concluded that population structure is maintained by small-scale habitat associations limited to a single estuary, supporting a hypothesis of demographic isolation among estuaries (Bradbury et al. 2008).

3.1.5 Combined methods

Natal site fidelity of the northern redbelly dace (*Phoxinus eos*), a North American freshwater minnow, was examined by combining ecological and genetic approaches (Massicotte et al. 2008). A 2-year mark-recapture experiment conducted at four sites separated by 50–450 m strongly supported site fidelity during the reproductive period. Individuals recaptured at their marking sites were also characterised with five microsatellite loci, revealing that the fish from different sites significantly differed from a single genetically uniform population, thus confirming the homing behaviour. Straying rates were low, with most straying occurring between nearby sites. Considering the high population density of dace, their high swimming capability, their continuous distribution along the littoral zone, the distribution of the spawning sites, and the small size of the lake studied, natal site fidelity was strongly suggested in this species. These results are consistent with other studies that report high levels of natal site fidelity in freshwater fish species using tagging and/or genetic methods, e.g., smallmouth bass (Ridgway et al. 1991), northern pike (Miller et al. 2001).

3.2 Elasmobranchs

A review of evidence for philopatry in sharks, produced by Hueter et al. (2005), identified several conventional tagging studies showing that adults generally returned to the same

mating or pupping grounds year after year. It was acknowledged, however, that such studies provide no information on natal fidelity.

3.2.1 Telemetry

Passive acoustic telemetry tags were used to monitor the movement patterns of neonate blacktip sharks in their natal nursery, a small semi-enclosed bay inside a larger estuary (Heupel & Hueter 2001). Of the tagged pups that migrated out of their nursery in autumn, 30% (3) of pups tagged in 2000 and 50% (2) of 1999-tagged pups were reacquired by acoustic monitors inside the natal nursery area in 2001. The reappearance of these animals indicated a significant number of the pups surviving their first summer in the natal nursery area returned to that same nursery in subsequent years. Given the natural and fishing mortality that the juveniles must be exposed to during their winter migrations, as well as the limitations of acoustic transmitter battery life and other technical considerations, these rates of return are indicative of a relatively strong degree of natal fidelity, at least for juveniles.

3.2.2 Genetics

Molecular genetics has been used to test for natal philopatry against a background of large-scale seasonal movement in sharks. By measuring the variance in allele frequencies among reproductive groups (F_{ST}) and by assuming a specific model of gene flow and population structure, the number of interbreeding migrants per generation among reproductive groups can be estimated. Nuclear and mitochondrial (mt) DNA markers differ in inheritance pattern and can produce vastly different F_{ST} values in some circumstances. Nuclear markers are equally inherited from both male and female parents while mtDNA is passed directly from females to offspring of both sexes without any transmission from the male parent. Large F_{ST} values in mitochondrial but not nuclear markers are often taken to indicate higher fidelity in females than males to particular groupings or reproductive locations. Mitochondrial DNA and nuclear (four microsatellite loci) allele frequencies were measured in juvenile blacktip sharks from four widely spaced nurseries along the Atlantic and Gulf coasts of North America (Keeney et al. 2003; Hueter et al. 2005). The overall F_{ST} value for the mitochondrial marker was highly significant ($F_{ST} = 0.111$, $P < 0.001$) and much larger than the nonsignificant F_{ST} value for microsatellites ($F_{ST} < 0.001$, $P = 0.316$). The strong signal in the mtDNA data indicates that females return to the same region for parturition while the lack of signal in nuclear markers indicates a greater degree of male gene flow among regions. However, at a finer scale, comparisons among three nurseries separated by 100 to 250 km along the Florida Gulf coast failed to detect significant F_{ST} values for either mtDNA or nuclear markers. Thus, while female blacktip sharks exhibit regional philopatry, there appears to be considerable straying among adjacent nursery areas. However, these results are perhaps not surprising given the limitations of gene frequency data. If the majority of females return to the precise location of their own parturition but a small percentage of females stray to nearby nurseries, the resultant F_{ST} value will be too small to detect.

In other shark species, genetics has indicated strong to moderate signals of philopatry, e.g., lemon sharks (Feldheim et al. 2002), white sharks (Pardini et al. 2001), shortfin mako shark (Schrey & Heist 2003), scalloped hammerhead shark (Chapman et al. 2009). The generally occurring pattern is as described above for blacktip sharks, i.e., non-roaming or returning females and roaming males.

3.2.3 Combined methods

Recent research involving sharks is combining a variety of methods to develop a more complete picture of population structure and migratory cycles. Jorgensen et al. (2011) combined satellite tagging, passive acoustic monitoring and genetics to show how eastern Pacific white sharks adhere to a highly predictable migratory cycle. Individuals persistently

return to the same network of coastal hotspots following distant oceanic migrations and comprise a population genetically distinct from previously identified phylogenetic clades.

3.3 Marine teleosts

3.3.1 Coastal ecosystems

Natural geochemical signatures in otoliths were used to determine natal sources in weakfish (*Cynoscion regalis*), an estuarine-spawning marine fish, in eastern North America (Thorrold et al. 2001). Adults migrate annually off the east coast of the United States between their overwintering grounds in the south to spawning locations in estuaries and coastal embayments throughout the range of the species (Florida to Maine) in spring and summer. Larvae and juveniles are generally retained within natal estuaries until migrating to overwintering grounds in the autumn. Juveniles collected in 1996 were assigned to natal estuaries using linear discriminant function analysis parameterized with $\delta^{13}C$, $\delta^{18}O$, Mg:Ca, Mn:Ca, Sr:Ca, and Ba:Ca values in otoliths (Thorrold et al. 1998). Subsequently, 2-year-old spawners were sampled two years later when they returned to the estuaries, and were classified using the same parameters derived from analyses of otolith cores. Spawning site fidelity ranged from 60 to 81% in the five estuaries (Thorrold et al. 2001). Straying was largely confined to locations adjacent to natal estuaries, so was not due to a complete breakdown of homing behaviour. Given the lack of larval dispersal, connectivity rates are primarily determined by the propensity for adult fish to return to their natal estuary to spawn. Although natal fidelity rates were relatively high, there was still too much straying to demonstrate genetic differentiation through analyses of allozymes and mtDNA (Cordes & Graves 2003).

Thorrold et al. (2006) described a technique for transgenerational marking of embryonic otoliths based on maternal transmission of ^{137}Ba from spawning females to egg material. Females were injected with a $BaCl_2$ solution that was highly enriched in ^{137}Ba and depleted in ^{135}Ba as compared to natural barium isotope values. The barium is ultimately incorporated into the otoliths of embryos produced by an individual that has been exposed to the isotope. Almany et al. (2007) used the technique to mark the larvae of the benthic-spawning orange clownfish (*Amphiprion percula*) and the pelagic-spawning vagabond butterflyfish (*Chaetodon vagabundus*) on a reef system (0.3 km^2) surrounding a small island. The work aimed to investigate the degree to which fish populations are connected by larval dispersal. Sampling subsequent to the marking indicated that about 60% of juveniles of both species that settled on the reef had been spawned there, providing evidence that larvae that spend 10–40 days in the pelagic environment are capable of returning to a very small target reef.

3.3.2 Open ocean ecosystems

Studies demonstrating spawning ground identity in an open ocean environment are even more difficult because the environments are less distinct and more variable among years than freshwater or coastal systems. Thorrold et al. (2002) reviewed artificial and natural tagging methodologies that could be used to track larvae throughout the pelagic larval phase and subsequent recruitment into benthic populations. One artificial approach is the immersion of embryos or larvae in marker chemicals that are incorporated into body tissues (e.g., fluorescent compounds, elemental tags, and radioactive isotopes) to mass-mark individuals. However, the mark longevity of these methods is generally less than a year, so while they may be useful to study the source of newly settled juveniles (as shown by Almany et al. (2007) using ^{137}Ba) they have little applicability to determine the natal origin of adult spawners. A second artificial approach produces physical marks in structures that are influenced by environmental perturbations, e.g., the thermal signals represented by daily growth ring patterns in otoliths, as used to mass-mark batches of salmon (Volk et al. 1990). Natural tagging methodologies identified by Thorrold et al. (2002) were genetic markers,

geochemical signatures in calcified structures, meristic or morphological variation, and physical marks in structures caused by environmental variations. All these methods are described in this review in relation to particular species studies.

The Atlantic cod has been the subject of many tagging studies and some populations clearly exhibit repeated homing to spawning grounds, i.e., adult spawning fidelity (Robichaud & Rose 2004 and references therein). Recent studies have provided evidence of spawning-site fidelity at a very fine spatial scale (less than 1 km) in coastal regions where barriers to dispersal exist (Skjæraasen et al. 2011). Population separation may even be maintained at overwintering grounds (Campana et al. 1999). Using archival tags in sub-adult and adult fish, Svedäng et al. (2007) demonstrated non-random, directional movements in agreement with the hypothesis that the northeast Atlantic cod population comprises a mixture of resident and migratory stocks. The authors concluded that their findings implied that natal homing was the mechanism that defined the stock structure of Atlantic cod. However, this was disputed by Bradbury & Laurel (2007) who noted that Svedäng et al. (2007) had ignored the true 'natal' component of dispersal (i.e., the egg and larval phase). So a more parsimonious hypothesis is that individuals are imprinted during the juvenile stage and homed to spawning regions on or nearby nursery areas rather than to natal locations.

Variation in microsatellite DNA loci provided evidence of genetic structure among Atlantic cod populations in the northwest Atlantic (Ruzzante et al. 1998). Differences were apparent both at the continental shelf scale and at the spawning-bank scale. The smaller scale differences were consistent with postdispersal spawning fidelity to natal areas, a behaviour that is possibly facilitated by topographically induced gyre-like circulations acting as retention mechanisms. Otolith core chemistry (i.e., an analysis of Ba, Mn, and Sr) was used to determine the juvenile source of spawning cod in Icelandic waters (Thorisson et al. 2011). The spawners born in 1997 (a year of high water inflow into the shelf area north of Iceland that mixed the juveniles from different areas) were not backtraceable to their origin, while most of those from the 1996 year class (a year of more normal current flows) were backtraceable. While neither Ruzzante et al. (1998) nor Thorisson et al. (2011) claimed to have demonstrated natal fidelity, their studies do demonstrate how the respective investigation methods (which have potential to test for natal fidelity) can be influenced by oceanographic features and processes. Clearly, such techniques may be useful to backtrace the origin of spawners in areas with limited mixing, but less well suited for areas or years of high current velocity or complex mixing.

Atlantic bluefin tuna have distinct spawning and nursery areas in the eastern (Mediterranean Sea) and western (Gulf of Mexico) Atlantic Ocean. Rooker et al. (2008a, b) examined the chemical signatures of $\delta^{13}C$ and $\delta^{18}O$ in the otoliths of yearlings from the two nurseries and found them distinct. Thus, they serve as natural tags to assess natal homing and mixing. Natal homing, defined by the authors as the return of spawning adults to their region of origin, was high for both eastern (96%) and western (99%) spawning regions. This work corroborated earlier indications of spawning fidelity from electronic tagging data that showed return migrations of both Mediterranean and Gulf of Mexico spawners over multiple years (Block et al. 2005). However, similarly to the Atlantic cod investigations, Rooker et al. (2008a, b) ignored the ichthyoplanktonic dispersal phase of bluefin tuna. So while this work shows that there is a very strong likelihood that mature tuna will return to spawn near their nursery area, it has not conclusively demonstrated natal fidelity (under the definition stated at the start of this document). However, it could be argued that given that there are only two spawning areas, each on opposite sides of the Atlantic, it is not necessary to show a return to the exact location where a fish was spawned to claim proof of natal fidelity. For a review of how otolith science has informed migration and stock structure theories on bluefin tuna, see Secor (2010).

4. ASPECT OF HOKI BIOLOGY RELEVANT TO NATAL FIDELITY

The main spawning grounds are centred on the Hokitika Canyon off the WCSI and in Cook Strait Canyon. However, spawning is also known to occur at other locations, e.g., Puysegur Bank, northern Pegasus Bay. The planktonic eggs and larvae move inshore by advection or upwelling (Murdoch 1990; Murdoch, 1992) and are widely dispersed north and south with the result that 0+ and 1-year-old fish can be found in most coastal areas of the South Island and parts of the North Island. The major nursery ground for juvenile hoki aged 2–4 years is along the Chatham Rise, in depths of 200 to 600 m. The older fish disperse to deeper water and are widely distributed on both the Sub-Antarctic and Chatham Rise. Analyses of trawl survey (1991–2002) and commercial data suggests that a significant proportion of hoki move from the Chatham Rise to the Sub-Antarctic as they approach maturity, with most movement between ages 3 and 7 years (Bull & Livingston 2000, Livingston et al. 2002). Based on a comparison of *Tangaroa* trawl survey data, on a proportional basis (assuming equal catchability between areas), 80% or more of hoki aged 1–2 years occur on the Chatham Rise. Between ages 3 and 7, this drops to 60–80%. By age 8, 35% or less fish are found on the Chatham Rise compared with 65% or more in the Sub-Antarctic.

The results of a pilot study to investigate the core signatures (elements and stable isotopes) of hoki otoliths from the 2000 and 2006 year classes caught on the Chatham Rise and in the Sub-Antarctic are currently being written up (Francis et al. in prep.). In summary, the study found considerable heterogeneity in core signatures. However, there is evidence that the average chemical composition of the inner otolith (up to the first annual zone) of fish from the 2006 year class differs between the two areas. There was also evidence of significant differences in the composition of the inner otolith between fish from the two year classes caught in the same area in the same year. The overall results were not consistent with the hypotheses of either complete natal fidelity or no natal fidelity.

What level of spatial resolution is necessary before it can be concluded that a fish exhibits natal fidelity? Take, for example, a fish that is spawned in a particular sea-grass bed in a distinct bay within an estuary, and it initially spends some months in that estuary before migrating to the open sea. Does it exhibit natal fidelity if it returns to spawn in the same estuary, or in the same bay within the estuary where it was spawned, or to the actual sea-grass bed in the bay in the estuary where it was spawned? It can be argued that natal fidelity is exhibited in all three scenarios. Clearly, the extent to which it is believed that natal fidelity is being exhibited by a species will probably vary depending on the knowledge of the size and distribution of spawning grounds.

For hoki, what would we need to show to conclude that the species exhibits natal fidelity? We know that there are two main spawning grounds (WCSI and Cook Strait), although spawning also occurs at other locations. So we would need to show that a high proportion of fish originating off WCSI return there to spawn, and a high proportion of fish originating in Cook Strait return there to spawn. Ideally, we would also demonstrate similar high degrees of fidelity to some of the minor spawning grounds as well.

5. SYNTHESIS OF METHODS TO DETERMINE NATAL FIDELITY, AND THEIR APPLICABILITY TO HOKI

To follow a fish from its egg or larval stage to spawning maturity it is necessary to mark it in some way so it can always be identified later in its life. Marks, or tags, can be acquired naturally or artificially. Details of possible methods, and how they might be applicable to an investigation of natal fidelity in hoki, are listed below.

5.1 Artificial tags

- Physically applied tags. These include 'classical' external tags or acoustic tags, and internal tags (e.g., coded wire tags). Clearly, these can be used only to mark post-larval teleosts or post-partum elasmobranchs. Consequently, unless the juveniles of a species are known to remain on or very near the grounds where they originated, these techniques are of little use in studies of natal fidelity. Also, the relatively high rates of larval and juvenile natural mortality means that huge numbers of fish would need to be tagged to ensure the later recovery of tagged spawning adults.

  It is not practical to apply this method to hoki as there is no possibility of obtaining, treating, and releasing healthy specimens of newly hatched larvae or juveniles. Also, the frequent occurrence of relatively strong currents at the main spawning grounds could result in the juvenile fish being a considerable distance from their natal area before they are big enough to undergo any tagging procedure.

- Fin clipping. Similar to external tags, this method is useful only if the juvenile fish are known to remain on or very near the grounds where they were spawned. Again, huge numbers would need to be treated to ensure some recaptures at maturity.

  It is not practical to apply this method to hoki as there is no possibility of obtaining, treating, and releasing healthy specimens of juvenile fish. Also, water currents are likely to have moved the juveniles away from their natal area before they are big enough to be fin clipped.

- Biochemical tags in otolith cores. This is achieved either by inoculating the brooding female with concentrations of an isotope that is uncommon in the natural environment and which is incorporated in her eggs, or directly exposing hatched larvae to an uncommon isotope. While it is possible to tag large numbers of larvae in this way (assuming females are accessible or the larvae can be confined), because of the very high natural mortality rates of eggs, larvae, and juveniles it is necessary to treat a high proportion of the females or larvae to ensure sufficient recaptures at maturity.

  It is not practical to apply this method to hoki as there is no possibility of obtaining, treating, and releasing healthy specimens of spawning females or newly hatched larvae.

- Modifying daily growth zone patterns to create 'bar-coded' otoliths. Newly hatched larvae are exposed to thermal variation, which produces a distinct bar-code pattern (of wide and narrow zones) in otoliths. Again, very large numbers of larvae must be tagged to overcome the high mortality rate of tagged fish and thus ensure sufficient recaptures at maturity.

  It is not practical to apply this method to hoki as there is no possibility of obtaining, treating, and releasing the large numbers of healthy specimens of newly hatched larvae required.

5.2 Natural tags

- Geochemical signatures in otolith cores. Many elements are incorporated in otoliths in approximate equilibrium with the concentration of the same elements in the ambient water. Consequently, if the chemical signature of the water differs between

two spawning areas then this will manifest as different biochemical signatures in otolith cores of fish originating in those two areas. The otolith cores of fish returning to spawn can then be analysed to determine their natal area. Clearly, this technique would work best when the spawning areas have relatively constant sources of current inflow and limited water mixing, thus ensuring minimal variation in the signature during a spawning season and between years.

Both the main hoki spawning grounds are in relatively open areas experiencing frequent strong current flows, and the spawning season extends over months. Hence, there would be considerable scope for between- and within-season variation in the chemical signature of the water at an individual spawning ground. If this method was used to investigate natal fidelity in hoki then any between-ground comparisons would need to be restricted to individual year classes, thus removing the effects of any between-year variation (as was done in the pilot study by Francis et al. (in prep.)).

- Daily growth zone 'bar-coded' otoliths. If newly hatched larvae are exposed to naturally occurring thermal variation, then a distinct bar-code pattern (of wide and narrow zones) can form in otoliths. However, this technique has little use as a natural tag unless the spawning season is very short (i.e., only a few days long). Where spawning occurs over a longer period it is not possible to identify a single 'bar-code' applied across the entire cohort because the natural variations in the thermal regime in one week are likely to be different to those in the following week.

  Testing for natural bar-coding in hoki otolith daily growth zones would not be practical as the spawning season is far too long, resulting in a wide variety of patterns in any one spawning season at a single ground.

- Developmental tags. Differences in larval growth history and genetics can result in either meristic or morphological variation between distinct spawning populations. For example, fish larvae can show temperature-dependent effects on the development of meristic characters such as the number of vertebrae, fin rays, or spines. However, for developmental tags to be useful at distinguishing natal fidelity of spawning populations, the environmental drivers must maintain relative consistency within a single spawning ground, and also maintain consistent differences between spawning grounds. Clearly, the driving factors often exhibit great spatial and temporal variability and therefore may not result in consistent 'marking' of larvae spawned from the same population. It is also possible that some of the differences could be driven by factors having an effect long after the fish have left their birth place (e.g., differences in the nutrition available at different non-spawning areas). In this situation, differences may indicate adult fidelity, but not natal fidelity.

  The use of developmental tags has been previously examined for hoki (Horn & Sullivan 1996; Livingston & Schofield 1996; Smith et al. 2001; Hicks & Gilbert 2002; Hicks et al. 2003). While some differences in growth rates were apparent between the adult spawning populations, differences in meristics were apparent for some, but not all cohorts. This work provided some support for adult fidelity in hoki, but not spawning fidelity. It is unlikely that the environmental and/or genetic drivers that produce developmental tags would be sufficiently constant within a single hoki spawning ground (given the relatively long spawning season, the known between-year variations in environmental conditions, and the apparent genetic homogeneity), or consistently different between grounds. Consequently, this method is also ruled out as having any potential to establish levels of natal fidelity in hoki populations.

- Genetic tags. Significant differences in the allozyme allele frequency at highly polymorphic loci would be indicative of essentially distinct spawning populations. Similarly, any analyses of mtDNA that produced significant differences would be indicative of a distinct separation in spawning groups (although for such an analysis it would only be possible to conclude female separation). However, genetic approaches generally have insufficient resolution to quantify natal homing unless straying is negligible over evolutionary time scales (and few studies have been able to demonstrate this).

  Searching for genetic tags in hoki is unlikely to be productive. Initial genetic approaches using allozymes found no significant regional differentiation (Smith et al. 1981). An analysis of polymorphisms in mtDNA of hoki from the two main New Zealand spawning sites and one spawning concentration off Tasmania found moderate levels of genetic diversity (Smith et al. 1996). However, the majority of the diversity was within samples from a single area; there was no significant genetic heterogeneity between areas.

6. CONCLUSIONS

Natal fidelity (or philopatry) is a behaviour whereby a fish always returns to spawn on the spawning ground where it originated. Hoki is certainly a problematic candidate for an investigation of natal fidelity. It is a relatively delicate deepwater species, so no artificial tagging methods could be successfully applied. Because it has multiple spawning areas, all in relatively open locales subject to strong but variable current flows, the species is likely to experience relatively rapid and variable dispersal of eggs and larvae from the natal areas, hence reducing the effectiveness of any natural environmental tags. The relatively long spawning season adds further complication in this regard. Consequently, in any year and between years, the eggs and larvae from any one spawning ground could be exposed to a wide variety of areas, water masses, and geochemical signatures.

The development of natal fidelity would be evolutionarily favoured as individuals that successfully survived, matured, and returned to their natal nursery areas to breed would be more likely to pass on their genes than fish that spawned in other areas that are seldom or irregularly used for spawning. These specific spawning areas would be positively selected because they were successful in producing fish that reproduced. If an area is not predictably better for successful spawning than an alternative, then natal fidelity need not exist. It might be expected that the selection for philopatry is likely to be greater in species with spawning areas that are enclosed geographically (i.e., freshwater, estuarine, or near-coastal species) than in dispersing, off-shore, pelagic species which may have more diffuse spawning areas. However, it is clear that regardless of the habitat or life history of the species, direct measurements of connectivity between fertilised eggs and subsequent spawners is challenging because larvae typically spend from days to months in the pelagic environment before seeking suitable habitat to begin adult life.

It is apparent that even in high-profile natal homers, such as salmon or other anadromous species, stray rates can be high (sometimes approaching 50%), and are variable over time. Proving natal fidelity for a significant proportion of adults in a marine population is very difficult, and has been achieved for few species. The habitat and behaviour of hoki places them in a group of species for which it is relatively difficult to maintain natal fidelity; they are an off-shore species, widely dispersed in the non-spawning season, with multiple, relatively diffuse spawning areas. It is safe to conclude that any hoki population model assuming 100% natal fidelity is untenable. Even if natal fidelity is the preferred option for hoki from an evolutionary perspective, it is almost inconceivable that a large proportion of the population

would not stray routinely. The preliminary results of Francis et al. (in prep.) indicate that hoki exhibit neither complete natal fidelity nor no natal fidelity (i.e., random 'choice' of spawning ground).

Based on meristic analyses, it seems likely that hoki exhibit adult fidelity. If they exhibit natal fidelity then we would expect unique signatures in meristic and other studies (e.g., otolith core chemistry), at least when comparing across the same year class; this has not been found. In any case, complete natal fidelity would not be expected in hoki (or any other open ocean species). It would be very difficult to determine what proportion of hoki does return to their natal ground to spawn. This proportion could be relatively constant over time (if it is driven by a relatively consistent 'desire' imprinted at the egg/larval stage), or could vary markedly (if it is related to environmental factors, relative density of stocks, or is simply a random 'choice' by the fish). Because it is likely that at least some hoki spawn in many of the canyon features around the South Island then multiple different natural 'tags' would be created in hoki from a single year class.

It appears that only one experimental method may be applicable and practical in any determination of the extent of natal fidelity by hoki, i.e., the analysis of geochemical signatures in otolith cores. Because of the relatively high levels of heterogeneity in core signatures (Francis et al. in prep.), sample sizes would need to be relatively large (to account for the multiple spawning areas) and comparisons involving numerous year classes would be necessary (to account for any between-year variations). Even then, it may still be difficult to detect sufficiently precise differences to enable the development of an accurate stock structure model. Clearly, the two extremes of the hoki stock structure model are 100% natal fidelity, and random choice of spawning grounds (presumably with adult fidelity occurring in both). Comparing the results from two stock assessment model runs, each assuming one or other of these two extreme stock hypotheses is perhaps the best currently available means of dealing with this uncertain aspect of the hoki life history.

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