Fish Migration and the Unit Stock: Three Formative Debates

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I. THE UNIT STOCK AND POPULATION THINKING

Modern fisheries science emerged through the early efforts of the International Council for the Exploration of the Sea (ICES) to understand factors that caused
fluctuations in important coastal fisheries (Smith, 1994; Smed and Ramster, 2002). A major research goal early on for ICES scientists was to establish relationships among fish distribution, behavior, and environmental factors (Nakken, 2002). Late nineteenth-century investigations on Atlantic herring by Heincke (1898) supported a widely held view that many local races structured the distribution of herring and their availability to fisheries. Local fisheries might then have local effects. This so-called modern migration theory displaced an earlier view of panmixia in cod and other coastal fishes. In contrast to these earlier ideas, ICES scientists discovered that fish became accessible to fisheries according to population renewal processes structured over large but distinct geographic regions (Hjort, 1914).

The unit stock arose as a means of practically defining vital rates and renewal rates pertinent to geographic regions where fisheries were undertaken. Early use of the term was by Dahl (1909), who defined stock as the source of fish. Later, Russell (1931), in his catch equation, defined stock as the exploitable portion of a population. Stock as an operational definition could be tailored for regions where vital rates and recruitment were deemed homogenous (Gulland, 1983; Cushing, 1995). Thus, while population thinking underlies the way we define and manage stocks, stocks themselves are not ecological entities per se; they are operationally defined by the geographic extent of anthropogenic effects and other practical considerations. Levels of biological structure relevant to stock issues can range from species to brood (Fig. 3-1). In some instances, lineage (species to population levels) may be critical in defining management units, as is the case when large reductions occur to abundance and threaten maintenance of the underlying gene pool. This often entails an evolutionary perspective that can extend millions of years and across ocean basins. In other cases, ecological time and spatial scales may be of greatest relevance. For instance, a manager may need to know how important a given habitat is as a source for recruits. Here, stocks are defined according to regions of production, and biological levels such as contingents, cohorts, and shoals may be important (e.g., Beck et al., 2001).

Despite the operational definition of stocks, there is little doubt that population structure is fundamental to how we assess and manage living resources (Sinclair, 1988; Sinclair and Smith, 2002). Population thinking arose during the early twentieth century as scientists contended with Hjort's discovery of population cycles common over large coastal regions (Solemdal and Sinclair, 1989). Issues remained as to which geographic scales were relevant to populations (scale and entity), which behaviors contributed to population structure (migration, life cycle closure, and philopatry), and the consequences of population structure (or alternatively, the consequence of deviations from life cycle closure). Here, I introduce three formative debates, which relate to pattern, process, and consequence. These include: (1) the effectiveness of cod hatcheries in fjords of southern
FIGURE 3-1. Temporal and spatial domains, and levels of biological organization relevant to the unit stock. Here, the unit stock is operationally defined by the anthropogenic effects of interest (Gulland, 1983).

Norway; (2) evaluation of the parent stream theory for Pacific salmon; and (3) the eel problem: Who contributes to population renewal processes?

II. DEBATE 1. EARLY COD HATCHERY ENHANCEMENT: LOCAL OR GLOBAL EFFECTS ON FISHERIES?

Johan Hjort’s pioneering observation of population response to periodically strong year-classes remains a principal paradigm that guides fisheries science and management. To make this revelation, Hjort and his team had to turn away from prevailing theory, which stipulated local races and local effects (Sinclair and Solemdal, 1988), and discover a new way of thinking about the renewal process. Several scientists and historians have argued that Hjort’s “population thinking” may have originated from practical considerations on the effectiveness of hatchery releases of larval cod into Norwegian fjords over a century ago (Solemdal et al., 1984; Sinclair and Solemdal, 1988; Smith, 1994; Schwach, 1998; Secor, 2002; Sinclair and Smith, 2002). Did these releases produce local effects in a fjord? Or were released cod swamped by natural juvenile production within the fjord or, perhaps, from outside the fjord?
By the mid-1890s the Flødevigen hatchery under the leadership of G. M. Dannevig was releasing millions of cod larvae into southern Norway fjords. Early development of egg fertilization and hatching led to the belief that "... cod fry artificially hatched have the power and energy to live, grow, and develop when set at liberty and left to care for themselves in their natural element, the sea" (Rognerud, 1887). From 1890 to 1906, 23.3 billion yolk-sac larvae were released into small fjords, sounds, and bays in southern Norway (Solemdal et al., 1984). Hjort questioned the effectiveness of these releases and a study was commissioned in 1903 by the Norwegian Parliament (Smith et al., 2002) that required the participation by both Dannevig and Hjort. Hjort assigned Norwegian scientist K. Dahl to work with Dannevig. During spring 1904 and 1905, millions of cod larvae were released into two fjords, and subsequent summertime juvenile abundances were estimated through beach seine sampling. These abundances were compared to summertime abundances in 1903, when no releases were made (Table 3-1). Dannevig reported increased juvenile abundances associated with the releases for 1904–1905 in comparison to 1903, the control year. Dahl, on the other hand, investigated other fjord systems that did not receive hatchery larvae in 1904 and 1905. In 1904, large numbers of juveniles were encountered in the fjords Dahl surveyed regardless of whether releases were made. But in 1905, the abundance of juveniles was relatively scarce in all fjords, again independent of whether larvae were released or not (Table 3-1). Dahl concluded (1909) that, "... the formation of the fish stock (the fish supply) in these fjords is not really much dependent on the spawning and hatching taking place in the fjord itself, it is more dependent on the quantities of fry brought by currents (the circulation of fry)." Thus, the same study resulted in conflicting conclusions. Parliament

<table>
<thead>
<tr>
<th>Year</th>
<th>Søndeled Fjord</th>
<th>Helle Fjord</th>
<th>Sandnes Fjord</th>
<th>Søyle Fjord</th>
<th>Christiania Fjord</th>
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<tr>
<td></td>
<td>Larvae released</td>
<td>Cod per haul</td>
<td>Larvae released</td>
<td>Cod per haul</td>
<td>Larvae released</td>
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<tr>
<td>1903</td>
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<td>6.3</td>
<td>0</td>
<td>5.4</td>
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<tr>
<td>1904</td>
<td>$33.5 \times 10^6$</td>
<td>33.7</td>
<td>0</td>
<td>10.9</td>
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</tr>
<tr>
<td>1905</td>
<td>$33 \times 10^6$</td>
<td>11.4</td>
<td>$10 \times 10^6$</td>
<td>1.5</td>
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*The study on the effectiveness used "cod per haul" (number of juveniles collected using beach seines) to index juvenile abundance among years for months of July and August. Dannevig emphasized interannual comparisons in Søndeled and Helle Fjords, 1903–1905, using 1903 as a control year. K. Dahl emphasized between Fjord contrasts in 1904 and 1905 using Sandnes, Søyle, and Christiania Fjords as controls. Data from Dahl, 1909 (p. 31).
assigned a committee to evaluate the opposing conclusions, which determined that the uncertainty in the findings dictated continued study. Hatchery releases of cod and juvenile monitoring continued into modern times, and the issue of the effectiveness of hatchery releases of cod into fjords remains a point of contention (e.g., Smith et al., 2002).

The diverging views on the effectiveness of hatchery releases, which persist today (e.g., Secor et al., 2000, 2002), center on scale. Dahl maintained that fluctuations in juvenile cod abundances had to be thought about at a spatial scale larger than a fjord. Dannevig subscribed to the modern migration theory, which prescribed restricted movements inshore and offshore by numerous local races (Heincke, 1898; Smith, 1994). Dahl (1909) specified the theoretical underpinnings of Dannevig’s program: “...the importance of the size of the waters was reduced by accepting the doctrine that each area of the sea, even the smallest, possessed its own tribe of fish. These tribes were supposed to be highly local during the whole life of the individuals. They were easily injured by overfishing and had to be replaced by the aid of man.” Based on his studies of differing stages of Norwegian coastal cod, Dahl (1909) thought it “just to consider the fish stock of a considerable stretch of coast as belonging to the whole of the area.”

How could relevant spatial domains be applied to issues of stock renewal? The answer came through migration studies. Because adult cod do not reside the year round in spawning or nursery habitats, ontogenetic and seasonal migration patterns were needed to link stage-specific distribution patterns. Through early tagging studies, Hjort (1909) confirmed seasonal migrations between Lofoten Island spawning grounds and far-off Barents Sea feeding habitats. For Atlantic herring, Hjort and his colleagues used “certificates of origin”—unique optical patterns of scale annuli—to chart the seasonal migrations to and from spawning grounds. Based on herring studies, Hjort argued that different stages or sizes of herring located in different regions were in fact members of the same population (Secor, 2002). Such studies, informed by the hatchery investigation, provided Hjort with the critical spatial domain needed to combine samples across relevant scales and observe decadal cycles in abundance of Norwegian herring (Hjort and Lea, 1914). Thus, Hjort used complex life cycles to reveal the spatial scale relevant to stock renewal processes. But how then were complex life cycles maintained? Resolution of this issue came with early studies of the parent stream theory in Pacific salmon.

III. DEBATE 2. THE PARENT STREAM THEORY: DIRECTED MIGRATIONS OR LOCAL WANDERINGS?

Prior to the twentieth century, naturalists, commercial fishermen, and anglers long wondered: Where do spawning Pacific and Atlantic salmon originate? Does
a stream's spawning run represent a random mixture of mature fish migrating in from the coast? Or, does each spawning run represent the return of a generation of salmon to their parent's stream? The specific migration and spawning behaviors associated with salmon reproduction would seem to represent adaptations that only lineage could guarantee. Thus, the parent stream theory became dogma well in advance of scientific evidence. Two central issues required resolution: (1) Do salmon home to natal streams? (2) Where do spawning runs of maturing adults originate—from distant oceanic waters or from regional coastal waters? For Pacific salmon, scientific investigations and debate related to these issues were concentrated during the first half of the twentieth century starting with C. H. Gilbert's important work on natural tags (circuli patterns in scales) and homing for sockeye salmon, and culminating with work on ocean migrations by the International North Pacific Fisheries Commission (Neave, 1964; Royce et al., 1968). Nevertheless, much research remains to be done on mechanisms of migration, which remain controversial (Hansen and Quinn, 1998).

Is homing to natal streams obligatory or facultative in Pacific and Atlantic salmon? With 100 years of hindsight, this may seem like a ridiculous question, but as the famous ichthyologist Jordan (1887) pointed out, "It seems more probable than parent stream theory that the young salmon hatched in any river mostly remain in the ocean, within a radius of 20, 30, or 40 miles of its mouth." This idea was in keeping with the modern migration theory, prevalent in Europe during the late nineteenth century, which viewed seasonal disappearances of diadromous and coastal fishes as restricted migrations to deeper near-shore coastal regions rather than the result of extensive ocean migrations. In this view, homing is not due to directed behaviors ensuring philopatry, but is due only to proximity.

A. Natural Tags

Gilbert provided early evidence for the parent stream theory in a series of reports on Fraser River sockeye salmon (1914–1919) with an early application of natural tags. Like his contemporary Hjort (1909, 1914), Gilbert developed a demographic approach based on annuli in scales to explain cycles of abundance. Further, like Hjort, he used scale circuli patterns during the first year of life as certificates of origin. Distinct frequencies of circuli that were associated with the early freshwater juvenile period occurred among tributaries and, on occasion, even within tributaries (Fig. 3-2; Gilbert, 1919). Comparisons between juveniles and adults captured at Fraser River spawning localities showed the same number of circuli corresponding to the freshwater juvenile period, leading Gilbert (1915) to conclude, "Examination of the scales had removed any possible doubt that the progeny of the Fraser River fish return to the Fraser at their maturity, and that this is true also of the fish of each of the large river basins."
FIGURE 3-2. Box-whisker plots of circuli counts of Fraser River juvenile sockeye salmon, collected in 1918 (Table III; Gilbert, 1919). Not shown due to low sample size ($n = 12$) is the Hanceville locality. Sample sizes for other sites ranged from 40 to 153. Letters represent similar and discrete statistical groupings (ANOVA; Tukey post hoc test; $\alpha = 0.05$).

Were these natural tags the result of environment or lineage? Gilbert argued for both causes. He believed that heredity fixed racial differences existed among tributaries, but also stated that "... during their life in freshwater salmon are subjected to obviously diverse external conditions. These are most marked perhaps, between salmon inhabiting different watersheds, but undoubtedly exist, if in less degree, between those that live for a year or more in different lakes belonging to the same river basin" (Gilbert, 1915). Although speculative, reconciliation of these two apparently diverging views may have come from Gilbert's appreciation for trait variance within species and populations: "... the peculiarities of each race in the matter of habitat do not lie outside but within the total range of variation as found in other river basins. Nothing new to the species, then, is found in a rare phenomenon, within the range of variation exhibited elsewhere" (Gilbert, 1914). Thus, Gilbert may have recognized well in advance of population genetics (e.g., Fisher, 1930) that heredity leads to modalities in trait expression rather than invariant race-specific traits.

To refute Jordan's criticism of the parent stream theory, it was insufficient to only recognize trait differences between tributaries—this could be due to local
ambits rather than philopatry. Initial evidence for philopatry came from observations of low straying rates between adjacent spawning tributaries. For instance, from many thousands of sockeye salmon examined from Rivers Inlet Race, only 24 were observed to exhibit different scale patterns, which were attributed to the adjacent Fraser River race. Gilbert (1917) concluded, “...the spawning runs in these streams and tributaries enjoy practical isolation, each from every other...”

The question of hatcheries underlay the early work on Pacific salmon, as it did with Norwegian cod. As previously described, Dahl (1909) and Hjort (1909) used the issue of scale to argue against local benefits due to local releases of cod. In contrast, Gilbert’s early work suggested that hatcheries could have local benefits. Gilbert (1915) advised that for hatcheries to be effective, “every stream must receive its own quota of fry.”

Using natural tags to evaluate philopatry entails a troubling conundrum. What if the salmon of two tributaries exhibit the same certificate of origin? Gilbert (1919) noted two possible causes: Racial segregation has not occurred, or segregation has occurred, but has not resulted in divergence in the natural tag. Gilbert and others (e.g., Neave, 1964; Harden Jones, 1968; see also Waldman, 1999) have used multiple phenotypic traits (e.g., growth, age at maturity, length of life in freshwater, color, quality of flesh) to reduce the chance that common certificates of origin for different races will be misinterpreted. Still, the parent stream theory entails lineage and natural tags can only provide circumstantial evidence. Later, Huntsman (1937a), a chief antagonist of the parent stream theory, would argue strongly against the use of natural tags in support of philopatry: “The characters that have been used to distinguish ‘races’ in species of marine fishes, such as herring and cod, are being demonstrated to result from the action of the environment on the individual during its lifetime, so that it seems doubtful whether there are heritable differences between the populations of different districts.”

B. MARKING EXPERIMENTS

Tagging should provide advantages in investigating homing because origins (spawning tributaries and localities) can be identified without the reliance of distinguishing natural tags. A central problem in early marking experiments for Pacific and Atlantic salmon was low rates of returning adults in comparison to tagged and released juveniles. Return rates of adults from a marked sample of juveniles ranged from 0% to 10% in early studies. What then happened to the majority of tagged juveniles? Were these lost due to straying to other systems, tagging and release mortality, mortality at sea, fishing mortality, or were they
somehow otherwise "lost at sea," as Huntsman and others believed? Interestingly, this debate remains important in investigations on homing mechanisms in salmon. Geolocation homing mechanisms entail high overall ocean mortality but efficient (>90%) homing by adult survivors (Quinn and Groot, 1984; Quinn and Dittman, 1990). Random walk models imply low ocean losses prior to spawning migrations, but less efficient (<10%) homing by adult survivors (Saila and Shappy, 1963; Jamon, 1990). Presumably in such models those adults that do not home, wander and are lost at sea.

In his compendium of migration studies, Harden Jones (1968) reviewed decades of early marking experiments, but highlighted the Cultus Lake experiment on Fraser River sockeye salmon conducted by Foerster (1936) as being instrumental in providing evidence for homing, and experiments conducted by A. L. Pritchard as evidence against substantial straying to adjacent tributaries. In successive years, Foerster's group marked (adipose fin clip) ~105,000 and 365,000 sockeye juveniles as they migrated seaward through a restricted outlet from Cultus Lake. For the larger release, a total of 12,803 returning salmon were recovered over a 3-year period. Of these, 71% were recovered from salmon canneries, which obtained salmon from commercial fisheries in coastal areas approaching the Fraser River. The remaining 2,856 fish returned to Cultus Lake. Thus, those salmon not captured in coastal fisheries homed to Cultus Lake.

Pritchard marked a portion (<5%) of pink salmon during their seaward migration from McClinton Creek in northern British Columbia (Queen Charlotte Islands) during the 1930s. In 1940, he examined returns in McClinton Creek and immediately adjacent streams for fin clips. In McClinton Creek, 781 of 35,521 (2.2 ± 0.1%) fish were marked. In four adjacent streams, only two marked fish were observed of 4,075 fish examined (0.04%).

Early marking experiments showed evidence for directed spawning migrations from coastal areas (Foerster, 1936) and lack of straying to adjacent streams. Still, these studies can show strong biases due to low recapture rates, unknown tagging effects, ocean and fishing mortality, and recapture reporting rates. Further, we still cannot confidently distinguish the role of proximity vs. philopatry. For instance, might the propensity of Cultus Lake sockeye salmon to home be due to the sampling domain, which did not include the ocean or coastal approaches to rivers other than the Fraser River itself? Further, subsequent tagging studies showed higher incidence of straying than indicated by the Pritchard study, leading Huntsman (1937b) to later question the prevalence of straying: "In quite a number of instances salmon marked or tagged in one river have been recaptured in another..." These issues would motivate a more manipulative approach to test straying rates by transplanting salmon across distant watersheds.
C. TRANSPLANT EXPERIMENTS

Many early transplant studies addressed practical issues such as restoring depleted runs or enhancing fisheries, but Snyder (1931) deliberately tested the parent stream theory by transplanting marked Chinook salmon juveniles of Sacramento River progeny into the Klamath River, and vice versa. Of 25,000 marked Sacramento juveniles released into the Klamath River, 10 were recovered at sea and 50 were recovered in the Klamath River. None of the 15,000 Klamath River juveniles released into the Sacramento River were recovered outside of coastal areas. This result was evidence that in one instance, spawning adults return to the stream in which they experienced their early growth rather than the stream where their parents resided. If the parent stream theory implied that progeny return to the stream of parents regardless of early rearing environments, then Snyder’s experiment and subsequent ones showing similar results refuted the popular theory. From a practical viewpoint, transplant and marking experiments did support the view that anthropogenic effects on spawning and rearing habitats of Pacific salmon would directly affect returns of subsequent generations.

D. THE YEAR-CLASS PHENOMENON (AGAIN)

Much like Norwegian and North Sea herring, region-specific recruitment cycles in Pacific salmon supported the view that populations were spatially structured. Contemporary to Hjort’s (1914) important observation of the impact of the 1904 year-class on Norwegian herring fisheries, Gilbert (1914) noted large interannual variation in Fraser River sockeye spawning runs with a 4-year dominant year-class cycle. Based on scales, differences in age structure were noted between the Fraser Rivers Inlet races. Gilbert attributed these cyclical patterns to differential reproductive success among years, which were tributary-specific. For the upper Fraser River, this cycle was interrupted by construction of a train corridor through Hell’s Canyon, which resulted in a large rock fall into the river (see Smith, 1994, for a review of this case study). Gilbert lamented that the 1917 spawning run “...was deprived to a large extent by the progeny of up-river spawners. ... Four years before, on their ascent of the river, these had been arrested at the canyon and died in the lower river without laying their eggs.” Here, local anthropogenic influences provided strong circumstantial evidence for the significance of homing on population dynamics. To varying degrees the localized influences of dams, hatcheries, pollution, and fisheries in spawning tributaries have a larger impact on anadromous salmon than other temperate coastal fishes due to the precise nature of their homing (e.g., Schaller et al., 1999).
While recruitment cycles and local effects showed that population structure was associated with homing within river systems, they did not provide support for the parent stream theory per se. We have yet to address the second issue prompted by the theory: Where do spawning runs of maturing fish originate?

E. Ocean Studies

In 1937, University of Toronto Professor A. G. Huntsman, in two letters to the journal Science, established himself as a principal skeptic of the parent stream theory. In particular, he was critical of the view that the return spawning migrations begin in distant ocean feeding grounds. “I maintain that the return of salmon to their native rivers from distant feeding grounds in the ocean is not only merely a theory, but one with a frail basis” (Huntsman, 1939). Huntsman’s view was similar to that of Jordan (see previously) and similar in concept to the modern migration theory of the late nineteenth century. Atlantic salmon (and presumably Pacific salmon) moved into coastal waters, proximate to the spawning river’s “zone of influence.” Once outside of this zone, salmon became lost and may have moved to other rivers or traveled out to sea. Very little was known about ocean distributions of salmon. Why should we expect salmon to occur outside of coastal waters where they were principally harvested? Understanding the oceanic occurrences of salmon would require a decade of concerted ocean studies, which came about due to the rapid emergence of ocean purse-seine and long-line fisheries for Pacific salmon.

Harden Jones (1968) cast Huntsman as a stalwart skeptic who presented important challenges and uncertainties to the widely held, but poorly supported parent stream theory. Indeed, Huntsman stated, “For questioning homing, I have suffered the fate of a heretic.” Still, Huntsman held a pretty high standard for this theory throughout his career. Initially, he argued against homing based on natural tag studies, suggesting that there was little evidence for directed homing migrations within tributaries (Huntsman, 1937a, b); then when presented with such evidence, he focused on uncertainties in oceanic migrations and the mechanism of homing: “Homing is a very definite feature in salmon migration, but it is the end of wandering rather than a directive factor” (Huntsman, 1950). And when multiple mark-recapture data showed that when an individual tagged as a juvenile occurred in distant ocean waters and then was recaptured as an adult in the natal river, Huntsman (1952) argued that “Recognition of home water does not direct the fish home, but may stop the wandering. Very foreign water may actually be avoided by the fish.” Huntsman held the view that while some salmon could home from distant waters, most did not. His contemporaries also thought that many salmon must be “lost at sea” (e.g., Saita and Shappy, 1963; Harden
Jones, 1968). Such views were in part reflective of a lack of directed studies on oceanic distributions of Atlantic salmon, a situation that would soon be remedied for Pacific salmon by the International North Pacific Fisheries Commission.

In 1955, a convention by fishing nations on North Pacific salmon (Canada, Japan, and the United States) formed the International North Pacific Fisheries Commission and initiated migration and distribution studies of salmon in the North Pacific Ocean and Bering Sea. Data and analyses from the resulting studies conducted in the late 1950s and early 1960s remain fundamental to knowledge and understanding of Pacific salmon oceanic migrations (Pearcy, 1992; Groot and Margolis, 1998). Further, these studies yielded a new dynamic understanding about salmon migration and oceanography. For Atlantic salmon, fishery-dependent mark-recapture studies on Atlantic salmon have occurred over the past several decades, but due to the limited scale of these investigations, patterns of oceanic distribution and oceanic migration circuits remain poorly understood (Hansen and Quinn, 1998).

Neave (1964) and Royce et al. (1968) summarized much of the Commission's research findings for pink, sockeye, and ocean-run steelhead, which included trawling directed at intercepting the migrations of juveniles, extensive mark recapture, and ocean fishery (purse-seine and long-line) data. These sources of evidence left little doubt as to the oceanic dependency of local races. Royce et al. (1968) described entire oceanic migration circuits, the underlying oceanography, and possible mechanisms leading to homing. These oceanic migration circuits occurred as single annual cycles for pink salmon, but were repeatedly undertaken as annual cycles by longer-lived salmon (Fig. 3-3). "Downstream" (confluent with major ocean current) migration circuits were described for British Columbia pink salmon in the Alaska Gyre; for eastern Kamchatka pink salmon in the current system centered on the Bering Sea and North Pacific Ocean; and for Bristol Bay pink salmon in the Bering Sea and North Pacific Ocean (Fig. 3-3). Neave (1964) focused on migration trajectories from oceanic aggregations to spawning grounds. Based on Japanese high sea fisheries data, he observed "... well ordered direction and timing of the movements towards appropriate spawning grounds..." and concluded that "... the evacuation of the high seas is not a random affair..." Thus, the weight of evidence from directed North Pacific studies countered the idea that salmon were lost at sea: "... we believe that the salmon's migrations could not be performed if they migrated or drifted at random..." (Royce et al., 1968).

F. THE PARENT STREAM THEORY and POPULATION THINKING

The parent stream theory or philopatry is a first principle in fisheries science. There is no more important assumption that underlies the management of fishery
stocks. As Huntsman and Harden Jones emphasized, the parent stream theory not only requires homing, but also requires a complex life cycle. A fish must leave natal areas to juvenile and adult habitats and then return. The spatial ambit and temporal frequency of this life cycle was codified in the migration triangle, conceived by Harden Jones (1968) and later modified by D. H. Cushing (Secor, 2002). For marine fishes, Cushing (1975) elaborated the migration triangle to include the concept of hydrographic containment, that life stages and migrations were constrained within oceanographic systems that favored denatant migrations of juveniles away from spawning areas and countrantant migrations by adults back to spawning areas (Fig. 3-4), a view favored by Harden Jones (1968) based on the many case studies he examined.

According to the views of philopatry and hydrographic containment, salmon were not lost or randomly cast about the oceans, but were distributed in time and space according to a complex life cycle designed to guarantee high levels of philopatry. Once such patterns were elucidated, recruitment cycles could be well matched with the influence of fisheries that were arrayed across the migration circuit. Similarly, other natural and anthropogenic influences that varied in time and space could be allocated in proportion to their effect on a given spawning population. The studies on Pacific salmon were taken as demonstrative of a general pattern for temperate and boreal marine fishes: “In temperate seas fish usually return to the same spawning ground each year at the same season, much as do Pacific salmon” (Cushing, 1995, p. 86).
Despite remaining issues related to the assumption of the parent stream theory and population substructure (see last section), marine fisheries research and management during the last half of the twentieth century moved to a typological view of stock structure and fish migrations. Migration studies and stock structure studies were directed at determining for each population a single spawning area, a single nursery area, and a single migration triangle (Stephenson, 2002). This approach has been substantially aided with the advent of biochemical markers, some of which represent population lineage and are thus more directly applicable to the issue of parental natality. An interesting late twentieth-century theory related to philopatry was the "member-vagrant" hypothesis (Iles and Sinclair, 1982; Sinclair, 1988), which countered the idea of denatant dispersal of juveniles, but rather emphasized the importance of larval habitats with physical retention features. Those larvae/juveniles that failed to arrive in prescribed nursery areas were "vagrants"—lost at sea. In this view, populations could persist only if spawning behaviors guaranteed that a large fraction of larvae arrived at nursery areas where retention would occur. Interestingly, Harden Jones doubted that single population circuits would survive generations. First, in consideration of homing migrations, "Homing could be a disadvantage when fish persist in returning to spawn in an area . . . where conditions have become unfavorable. . . . The only biological insurance against this is a satisfactory level of straying and a multiplicity of spawning grounds. . . ." Further, in consideration of population substructure, "the capacity to meet change lies, not in the flexibility of each unit, but the multiplicity of units." These observations were remarkably prescient of metapopulation and contingent concepts, which have only emerged during the past decade to meet some of the shortcomings of the parent stream theory.
IV. DEBATE 3. THE EEL PROBLEM: WHO CONTRIBUTES TO REPRODUCTION?

Population thinking in fisheries science largely developed outside ideas related to the role of races in natural selection (e.g., Darwin, 1859). Rather than evolutionary groups, races (populations) were conceived as ecological entities—groups of individuals that had common natality and migration patterns and were therefore affected similarly by exploitation, climate, and environment. Later, the widespread use of neutral lineage markers would depend on theoretical developments of microevolution. Still, stock structure studies were not explicitly related to evolution or speciation. Sinclair (1988) provided an initial theoretical basis for the role of evolution in stock structure by suggesting that population richness was itself a selected attribute, defined by oceanographic retention areas that favored larval survival. In addition, recent emphasis on conservation and biodiversity of aquatic resources has emphasized the relationship between population structure and endangerment of exploited species (e.g., Waples, 1995). Still, there remains little cross-fertilization between fisheries scientists and evolutionary biologists who work on fish (Conover, 2000). As recent evidence, consider that a series of papers devoted to the species concept in fishes, published in the journal *Fish and Fisheries* [Vol. 3(3); Stauffer et al., 2002], failed to address the role of population thinking in the species concept. Indeed, the journal issue did not contain a single reference to population or stock structure in fishes.

Within this dearth of studies on the species concept and population thinking in fisheries, there exists the so-called eel problem. During the past century, the linked problems of natality and migrations of Atlantic eels have required simultaneous thought about population structure and speciation. Indeed, debate on the role of population structure and speciation remains active for *Anguilla* species and important for their management (e.g., Tsukamoto and Aoyama, 1998; Tsukamoto et al., 2002).

Recurring as part of the resolution to the eel problem is the view that adult eels in major portions of their range do not reproduce (Tucker, 1959; Harden Jones, 1968; Tsukamoto et al., 1998), or that some eels disproportionately contribute to reproduction dependent on the habitats to which they recruit (Limburg et al., 2003). That some eels are destined never to reproduce seems a peculiar idea, but such proposals have been advanced for salmon due to ocean wanderings (see previously) and for vagrant fishes that range too far from their migration triangle (Sinclair, 1988). Might some juvenile/adult habitats and associated stocks require constant subsidy from reproduction from adults that grew elsewhere? Managing the effects of exploitation would engender risk if reproducers were selectively harvested or otherwise affected (Castonguay et al., 1994), an issue now attracting consideration in the design of exploitation refuges and marine protected areas.
A. MEDITERRANEAN VS. NORTH ATLANTIC ORIGIN OF EELS

Well after Aristotle's musings on spontaneous generation of eels in mud, evidence for the marine origins of eels began with the Italian naturalist G. B. Grassi, who recognized that Leptocephalus brevirostrum was in fact the larval form (termed leptocephalus) of Anguilla (Grassi and Calandruccio, 1897). Based on local collections of leptocephali, Grassi assumed that Anguilla spawned in the Straits of Messina (narrow straights north of Sicily). Proximity between inland freshwater fisheries for eels and coastal spawning areas (the modern migration theory) implied local populations of eels. "If Grassi's hypothesis was correct, there were likely to be problems of over-fishing if too many eels were trapped on their way to the sea, the implication being that each river was supplied by eelers derived from a local spawning ground" (Harden Jones, 1968).

Schmidt, through decades of directed ocean collections of the pelagic leptocephali, discovered that eels in the Mediterranean and North Atlantic originated in the Sargasso Sea (Schmidt, 1922). The Danish scientist's efforts in tracking ever-decreasing sizes of leptocephali across the Atlantic represented important pioneering research in fisheries oceanography (Jakobsson, 2002). Schmidt argued for a single spawning region in the Sargasso Sea for eel stocks throughout Northern and Southern Europe. Evidence against a separate Mediterranean spawning location included: (1) similar myomere counts for leptocephali captured in the Mediterranean with those captured in the Northeast Atlantic; (2) increased leptocephalus size inside the Mediterranean in comparison to outside the Mediterranean, implying older ages and longer periods of dispersal from the Sargasso Sea; and (3) earlier seasonal occurrences of leptocephali outside of the Strait of Gibraltar in comparison to those captured off Italy.

B. NORTH ATLANTIC EELS: SPECIATION OR POPULATION STRUCTURE?

That the European eel life cycle must include distant oceanic spawning in the Sargasso Sea was a surprising discovery; one not well accommodated by the emphasis of racial differences and population structure emerging from the ICES community (Hjort, 1909; 1914). If all eels, from the Baltic to the Mediterranean, were the result of spawning in the Sargasso and years of larval drift along the Gulf Stream, then all eel fisheries were dependent on one panmictic population: species and population were one and the same. Further, the Sargasso Sea not only included all European eel A. anguilla spawning, but also proved to be the only spawning region for the congeneric American eel A. rostrata. Indeed, in many of Schmidt's samples both species (distinguished by myomere counts) co-occurred as leptocephali. This finding presented a particularly difficult conundrum: Over
generations of presumed co-occurrence of spawning in the Sargasso Sea what led to maintenance of distinct eel species?

Schmidt's hypothesis was that leptcephali of European eels were entrained into the Gulf Stream and drifted for 2 to 3 years until they reached regions of Northern Europe (earlier) and the Mediterranean (later), whereupon they metamorphosed into glass eels and entered the estuaries and rivers of Europe. Juvenile habitats in North America were substantially more proximate to the Sargasso Sea, and leptcephali could be expected to reach most of these habitats within one year. Thus, if the leptcephalus development rates and stage durations were substantially different between American and European eels, then speciation might be maintained over generations. Evidence for this came from (1) drift bottle studies, which suggested leptcephalus drift must be substantially greater for eels arriving in European as opposed to North American estuaries; (2) European leptcephali that were over 33% longer at metamorphosis than American eels; (3) slower growth and development rates of European eels vs. American eels based on an assumed overlapping spawning season during spring (Harden Jones, 1968) (for instance, when European eels passed Bermuda, they were not competent to ingress into freshwater); and (4) sample sizes of \emph{A. rostrata} leptcephali collected by Schmidt that were substantially less than \emph{A. anguilla} leptcephali, corresponding to differences in fishery yields between the two species. (While early twentieth-century harvest records are probably insufficient to make this claim, production of European eels is likely higher. From 1980 to 2000, fishery yields were an order of magnitude higher for \emph{A. anguilla} in comparison to \emph{A. rostrata}.) Still, without direct observations of spawning eels, these lines of evidence only provided circumstantial support for speciation in North Atlantic eels.

C. Failed Adults

In an influential \emph{Nature} article, Tucker (1959) played the lone role of skeptic by suggesting an alternative set of explanations for regulation of eel stocks produced by Sargasso Sea spawning. Eel species were not distinct, but represented different phenotypes due to environmentally mediated meristic characters. He proposed that temperature differences across the large region over which small leptcephali had been observed in the Sargasso Sea could generate meristic differences in vertebral (myomere) counts. Different origins within the Sargasso Sea not only resulted in different dispersal fates (North America or Europe), but also associated vertebral counts. But this proposal was not the most controversial part of Tucker's thesis. He forcefully argued that the distance for adults to migrate from European waters to the Sargasso Sea was too vast. "European eels . . . do not succeed in returning to the ancestral spawning ground, but perish in their own
continental waters." Tucker believed that stocks of so-called European eels were sustained by American eel parentage. The idea of failed reproduction was similar to the view that much Pacific salmon production was lost at sea (see previously), but here stock structure of eels had consequence: If stocks failed in North America, so too would they fail in Europe.

A scientific debate on Tucker's proposal quickly emerged. Chief criticisms were against temperature affecting stable differences in myomere counts in American and European eels and Tucker's view that "... Europe and North Africa are regularly colonized by eels of American ancestry doomed to perish in a fruitless suicide-migration" (Tucker, 1959). D'Ancona (1959) argued that Tucker's hypothesis of temperature gradient differences would produce continuous variation in myomere counts rather than the observed bimodal pattern unless there was a threshold or critical temperature. Tesch (1977) and Harden Jones (1968) argued that expected temperature effects on vertebral counts from salmonid studies would lead to a difference of less than one vertebral count rather than seven, which would be required to explain the observed difference between European and American eels. In recent decades, karyotyping and other genetic studies (Passakas, 1981; Lintas et al., 1998) have determined the separation of species on grounds other than meristics.

The issue of whether European eels can successfully return to the Sargasso Sea has been more difficult to resolve and remains an active area of speculation. Tucker remarked that it was surprising that no emigrating silver (mature) eels had ever been observed in or near the Strait of Gibraltar. Others stated that the reason for an apparent absence of silver eels there and elsewhere was lack of fisheries and appropriate gear to observe returning eels (D'Ancona, 1959; Deelder, 1960). From an energetics perspective Tucker articulated this colorful metaphor: "... the advanced modifications of the European eel appear to be ill-adapted to ... a return journey. We may indeed know that a motorist is in the best of health but, as we watch him driving down a mountain road, intoxicated and without brakes, we can still legitimately say that his celebration was premature that he is likely to reach his destination." Did European eels have sufficient reserves to undertake a 3,000- to 4,000-km migration to the Sargasso Sea? Based on telemetry studies, Tesch (1977) argued that with a fat content of >20%, and using advantageous currents, an adult eel could accomplish a 6,000-km migration in 5 months.

More recent studies have failed to definitively resolve whether energetic stores are sufficient to undertake spawning migrations from waters as distant as the Baltic Sea. Svedäng and Wickström (1997) observed that many eels occurring in the Baltic Sea had limited fat reserves (<10%) and proposed that most of these eels may delay maturation and migration to the Sargasso Sea. Further, they believed that transformation to the adult silver eel form and related migration behaviors may be reversible. Van Ginneken and
vanden Thillart (2000) conducted swimming metabolism studies on large eels and predicted that only 40% of the total fat reserves of a 2-kg eel with a 20% fat content would be utilized for a 6,000-km spawning migration. Still, a 2-kg eel would represent an extremely large eel. For a more typical size of 500g, approximately 125% of fat reserves would be required to accomplish a 6,000-km spawning migration. Limburg et al. (2003) estimated a range of possible costs for eels of different sizes and origins, of which only a subset would be able to accomplish a 6,000-km spawning run based on energy reserves. While the issue of speciation in eels has been resolved through genetic studies, there remains the question of whether more distant yellow eel stocks such as those in the Baltic Sea substantially contribute to the pool of spawners.

D. “FRESHWATER EELS” AND CONTINGENT THINKING

*Anguilla* eels are commonly referred to as freshwater eels because it is assumed that their longest juvenile period, the yellow eel-phase, is dependent on freshwater habitats. Still, important fisheries are centered in estuaries (ICES, 2001), and scientists have suggested that brackish water regions may represent better growth habitats than freshwater systems (Helfman et al., 1987). In a recent letter to *Nature*, Tsukamoto et al. (1998) made the noteworthy discovery that some *A. anguilla* complete their life cycles without ever moving into freshwater. Further, based on a small sample of silver eels collected from the North Sea and using otolith microconstituent analysis, they concluded that freshwater eels did not contribute to the spawning population. Tsukamoto’s speculation on failed reproduction by freshwater eels was controversial, and subsequent analysis of a larger sample indicated that some Baltic Sea silver eels did in fact originate from freshwater eels (Limburg et al., 2003). Still, estuarine and marine eels made up the majority of these silver eels.

Tsukamoto et al.’s observation of divergent life cycles within eel stocks has been confirmed for several *Anguilla* species worldwide based on otolith microconstituent analysis (Arai et al., 2000; Tzeng et al., 2000; Tsukamoto and Arai, 2001; Limburg et al., 2003; Morrison et al., 2003). Thus, the issue of how freshwater vs. brackish and marine habitats contribute to reproduction is important for eel management, particularly because freshwater and estuarine systems are differentially affected by exploitation and habitat degradation (ICES, 2001). The observed modalities of individuals, within the same population, structured by discrete migration is well epitomized by eels, but in fact has been observed frequently for other marine species. Secor (1999) termed groups of individuals structured by lifetime migration patterns as contingents [the term *contingent* was based on early usage by Hjort (1914) and Gilbert (1914)] and proposed that
contingents represented important components of population substructure, particularly in strategies of spatially explicit fisheries and habitat management. This is exemplified by a recent proposal to establish exploitation refuges in freshwater eel habitats where little exploitation now occurs but could develop in the future (ICES, 2001). If freshwater contingents produce relatively few reproducing adults, then such a management strategy would prove ineffective (Morrison and Secor, 2003).

E. MORE EEL PROBLEMS AND POPULATION THINKING

The issue of speciation mechanisms for Atlantic eels has resurfaced in recent research. Wang and Tzeng (2000) observed hatch dates, which were fairly discrete for each species. Although differing substantially in season, direct observations of small leptocephali by McCleave and Kleckner (1987) also supported the view of allopatric spawning by *A. anguilla* and *A. rostrata*. While the assumption of daily increment formation in otoliths has not been substantiated, analyses indicate that dispersal is of much shorter duration for European eels (9–18 months) than suggested by Schmidt and other early investigators (Lecomte-Finiger and Yahyaoui, 1989; Wang and Tzeng, 2000). This shorter duration has called into question dispersal mechanisms for European eel leptocephali that now have an insufficient larval duration to allow transport by the Gulf Stream. McCleave et al. (1998) have proposed an alternative route by prevailing northeast flow from northeast regions of the Sargasso Sea.

In contrast to recent oceanographic and otolith studies, genetics studies have further muddied the picture of population structure in Atlantic eels. While *A. rostrata* remains consistently different from *A. anguilla* when genetic markers are used (e.g., Tsukamoto and Aoyama, 1998; Lehmann et al., 2000), Wirth and Bernardetzhe (2001) interpreted microsatellite DNA as evidence for population structure within *A. anguilla*. They observed a latitudinal gradient in genetic differentiation and suggested that population structure was maintained through differential seasonality in silver eel return migrations. In a second independent study, further evidence was given for nonrandom genetic structure of *A. anguilla* stocks (Daemen et al., 2001). Still, a more conservative genetic marker (mitochondrial DNA) showed genetic homogeneity of *A. anguilla* (Lintas et al., 1998), and the conclusion of population structure in Atlantic eels remains controversial, in part because it is difficult to conceive of a likely mechanism to retain population structure. Flaming controversy, an Italian scientist has sought to redeem history (Casellato, 2002): “[Recent genetic studies] could lead to support of . . . Grassi, who was convinced that European eels could reproduce in the Mediterranean Sea.”

The mystery of speciation and population structure in Atlantic eels will endure until spawning eels are captured (Tsukamoto et al., 2003). Issues of how eel
stocks contribute to overall reproduction remain very active and important, particularly as both species have experienced large declines in fishery yields during the past 20 years (ICES, 2001). The question of who reproduces, epitomized by eel investigations over the past century, has become critical as we become more reliant on management strategies of regional fishing allocation, exploitation refuges, and habitat protection. The eel example also demonstrates that such strategies may sometimes necessitate alternatives to "population thinking" (e.g., contingent and metapopulation thinking).

V. SUMMARY

These three examples of population structure in marine fishes support the strongly held views of Hjort and Gilbert that dynamics of living resources occurred within spatial domains defined by population migration circuits. There can be no doubt after decades of genetic study that salmon and most other marine fishes show varying degrees of homing. Fish commonly return to restricted spawning regions, and migration trajectories are seasonal and connect important reproductive, nursery, feeding, and winter habitats. Still, Hjort and Gilbert also noted an important source of biodiversity within the migration circuits. Nordland “fat” herring undertook a different migration circuit than the other Norwegian herring; a contingent of anadromous sockeye salmon did not partake in oceanic migrations. Later, Tsukamoto observed that some freshwater eels in fact persisted in marine waters throughout their life history. These deviations have been ignored during the first century of fisheries science, in part due to the view that populations are each defined by a single migration triangle (Secor, 2002).

Biodiversity in spatial behaviors within populations can have significant consequences on recruitment rates to regional fisheries, efficiency of hatchery enhancement programs, anthropogenic effects due to degraded or lost habitats, exposure of fish to contaminants, and overall resiliency of a population or metapopulation to longer term climate or anthropogenic change. Here, Book’s (1981) call to operationally define stock based on the issue at hand is prudent. Regardless of the complexity of population structure, stock can be defined at scales appropriate to the question at hand. Still, an increased focus on resiliency and conservation by policy makers and managers will mean that stock definition will encompass a broader perspective in space and time (Fig. 3-1). Further, many of the assumptions underlying population thinking remain unverified or inadequate. Consider the following:

1. In several presumably large subocean basin populations, it is increasingly evident that local renewal processes may be important to population and metapopulation resiliency. Large temperate fisheries for Norwegian spring-spawning herring, Japanese sardine, and Scotian Shelf Atlantic
cod have all experienced severe range contraction into local coastal or shelf regions during nadirs of population abundance (Hutchings, 1996; Watanabe and Wada, 1997; Holst et al., 2002). Thus, during decadal phases of collapsed abundance, local subpopulations may be critical as sources for the next population expansion. Also, through use of oceanographic models and otolith microconstituent analysis, retentive life cycles ("self-recruitment") have been observed in pelagic spawning species despite the large potential for advection, drift, and straying (Jones et al., 1999; Thorrold et al., 2001; Swearer et al., 2002; Sponaugle et al., 2002). Thus, local processes may be important in sustaining large opensystem populations.

2. Knowledge of the underlying mechanism of homing is incomplete for salmon and unstudied for the vast majority of fishes managed as unit stocks. For salmon, Great Lake studies support the role of olfaction as a local/regional means for identifying natal stream (Hasler and Scholz, 1983), but mechanisms of oceanic migration remain unknown and speculative (Hansen and Quinn, 1998). Still, rapid progress is being made in the use of electronic tags in oceanic migration studies, which may provide critical clues about possible homing mechanisms (Friedland et al., 2001). Indeed, the lack of a certain homing mechanism in salmon has kept Huntsman's views of oceanic wanderers alive (Jaman, 1990; but see Quinn and Groot, 1984, for evidence against this view). Thus, in salmon and other marine fishes there remains no complete explanation for the most important process underlying the unit stock—philopatry.

3. The emphasis on natural and lineage markers in defining the unit stock has not always provided useful resolution in stock structure issues. The confusion in using different types of markers should highlight that stock is not always clearly defined (Begg and Waldman, 1999). Also, markers result from processes that range in scale from ecological to generational to evolutionary (Waldman, 1999). Thus, defining stock in an operational manner should dictate which markers are used (phenotypic vs. lineage), rather than vice versa. Further, we should not take the term stock to be synonymous with population, as has been done in the past (e.g., Booke, 1981; Pitcher and Hart, 1982). Stock (Schmidt, 1909: "source of fish") is a specific portion of a population that is influenced by an anthropogenic activity that affects population productivity (Russell, 1931; Ricker, 1975; Secor, 1999). Similarly, tests of the parent stream theory using natural or genetic markers do not test the same assumptions related to natality—natural tags focus on source habitat; genetic markers focus on source lineage. It should be noted that the use of natural tags and electronic tags in recent years has seen rapid progress in better tests of homing in marine fishes and in more precisely quantifying anthropogenic
influences on fish populations (e.g., Block et al., 1999; Zlokovitz and Secor, 1999).

4. Alternative migratory pathways remain poorly accommodated in fisheries and habitat management. Unusual occurrences that were previously viewed as anomalies, strays, or vagrants were ignored because they did not match expectations for a given migration circuit. The "multiplicity of units" within a population (Harden Jones, 1968) or contingent structure was recognized early but forgotten for many decades, which favored research and management directed in support of a more monolithic view of migration—the migration triangle. The role of contingents and strays in fishery problems has again emerged with the advent of changed management goals and new stock identification methods (Secor, 1999; Secor et al., 2001; Limburg et al., 2001; Tzeng et al., 2000).

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