NAFO Sci. Coun. Studies, 6: 63–71

Parasites as Natural Tags for Marine Fish: a Review*

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Abstract

Management of exploited stocks of marine and anadromous fish requires understanding of the subpopulation structure and migratory characteristics of the species. Parasite tags have been used, along with other methods, to provide information on these topics. This brief review emphasizes examples of successful application of parasite tag techniques to redfish, cod, whiting, herring and salmon populations and summarizes other studies of parasites in haddock, plaice and winter flounder. General findings are that the method is most useful when long-term studies of persistent parasites are feasible, when concurrent ecological studies are conducted, and when alternative approaches to subpopulation distinctions or movements of stocks are available simultaneously.

Introduction

Parasites have been used to provide information about taxonomic relationships, migrations, and intermingling of terrestrial animals, particularly birds, for almost a century. Exploration of parasitological approaches to understanding populations and movements of marine fishes is of more recent origin, probably beginning with the work of Dogiel and Dykhovski (1939), who distinguished between two groups of acipenserids in the Caspian Sea, and the work of Herrington *et al.* (1939) on populations of redfish, *Sebastes marinus*, in the Gulf of Maine. The use of parasites as natural tags for fish was expanded greatly during the 1950's and has had continuing application ever since. In the past 30 years, the utility of parasitology to fishery biological and management needs has been demonstrated for a number of economically-important species, particularly salmon and herring but also redfish, flounders, cod, whiting, plaice, haddock, and others. Parasites which have provided the most definitive information include myxosporidians, encysted larval helminths, and parasitic copepods.

This paper attempts to review and assess progress in the application of parasitology to questions about discreteness of stocks and movements of marine and anadromous fishes. In view of the voluminous literature on the subject, much of the content of this paper is confined to specific examples of successful use of this approach.

Criteria for an Appropriate Parasite Tag

Parasites might, on superficial examination, seem to be unlikely prospects as tags for fish. Their life cycles are often complex or still unknown, their ecology which involves one or more hosts and the external environment is even more complex, and their identification is often uncertain or subject to disagreement. Despite these negative aspects, an ideal natural tag may be described as possessing the following characteristics:

1. Significant geographic variation in prevalence should exist, the parasite being common in one population and uncommon or rare in another.
2. The parasite should be detected easily, preferably by gross examination.
3. The life cycle of the parasite should preferably involve only a single host.
4. Definitive identification of the parasite should be feasible, as should identification of the host species and any subspecies.
5. The parasite should have a minimum effect on survival of the host.
6. Parasite prevalences should remain relatively stable from season to season and year to year.
7. The parasite should persist in the host for at least the duration of the study period (suggested minimum of 2 years) and preferably longer.

A natural tag with all of these attributes is rarely achieved, and compromises must be made. Less-than-optimum geographic differences in prevalences may not eliminate a parasite from consideration, and a complex life cycle involving more than one host may not be a basis for discounting the use of larval helminths. Departure from the ideal may be offset by the use of several different parasites simultaneously and appropriate multivariate statistical procedures, both in sampling design and data analysis.

* Presented at the Special Session on "Stock Discrimination in Marine Fishes and Invertebrates of the Northwest Atlantic", held at the Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada, during 8–10 September 1982.

Use of Parasites as Tags

In planning a program to elucidate populations or migrations of fish, each potential approach (i.e. parasitological, morphometric-meristic, biochemical-serological or artifical tags) should be examined with respect to expertise, time and funds available. The advantages of parasitic tags include the following: the method does not induce major or traumatic external effects on the fish because no handing is involved; the method can be combined with, and is enhanced by, biochemical serological and morphometric-meristic studies of the same samples; the method can be further enhanced by work on parasite biochemical speciation or strain differentiation; a larger proportion of the population is tagged than would be feasible with artificial tags (although the parasite tag is less specific than a coded artificial tag); the fish needs only to be caught once; and the cost of the study is usually less than that of a tagging program.

Parasites can provide information useful to solution of biological problems or useful to management of stocks, but limitations do exist. Training and background in parasitology is required of the person who plans and institutes the program. Extensive preliminary work is required to identify the parasites that are found, to determine if geographic differences in prevalence exist, and to learn as much as possible about the ecology and life cycles of parasites selected as candidates. This phase is particularly important if the parasitology of the host fish species is poorly understood. Parasite tags are unsuited for study of movements of individual fish. Correct identification of large numbers of parasites must be made throughout the study. For some larval helminth parasites, this can be a difficult and time-consuming occupation. Furthermore, each year-class of the fish hosts must be considered as a separate entity, and any study should encompass at least three year-classes. Also, a baseline parasite survey should be made of each population sampled at the time of spawning.

Successful Use of Parasites as Tags

The world literature on parasites as natural tags for marine and anadromous fish is extensive, addressing many problems in many species. Instances of successful application of the method to some of the important commercial species are summarized in Table 1. Of these, several seem particularly illustrative of solutions to specific problems.

Redfish stocks in the western North Atlantic

One of the most exhaustive surveys of parasite prevalences in redfish was reported by Templeman and Squires (1960). Working exclusively with the parasitic copepod *Sphyrion lumpi*, the authors found a major center of infestation off southern Labrador, with lesser centers on the southeast slope of Grand Bank and in the southeastern Gulf of St. Lawrence. The parasite was rare or absent in other areas, indicating limited intermixing. A study of residual remains of previous generations of the parasite (dead encapsulated heads) in the flesh of redfish disclosed the same centers of abundance as for living copepods, except for some spreading toward deepwater areas.

A less extensive study of redfish by Sindermann (1963), using a composite of frequencies of five different parasites, also indicated slight, if any, intermixing, even for stocks not widely separated geographically.

Cod stocks in the western North Atlantic

Early tagging studies (Schroeder, 1930; Wise, 1958) indicated a discrete, self-contained stock of cod in the area south of Nantucket Shoals, but other groups in the New England area were less clearly defined. Sherman and Wise (1961), using the parasitic copepod *Lernaeocera branchialis*, confirmed the discreteness of the southern New England population, which was free of infestation by the parasite. An increasing gradient of parasite prevalence extended northward. Light infestation of cod on Georges Bank indicated little mixing with the southern population or with populations to the north where prevalences were much higher.

Differentiation of North Sea whiting stocks

Two species of gall-bladder inhabiting myxosporidians, *Ceratomyxa arcuata* and *Myxidium sphaericum*, were used by Kabata (MS 1959, 1963a, 1963b, 1967) to distinguish northern and southern stocks of North Sea whiting. Fish north of 56°N were predominantly infected with *C. arcuata*, while those south of 54°N were infected mainly with *M. sphaericum*. The zone of overlap (54° to 56°N), which includes Dogger Bank, was delineated by intermediate prevalences of both parasites. The parasitological evidence also indicated the existence of a distinct whiting population in the Irish Sea.

A later study by Hislop and MacKenzie (1976), using conventional tags and the distribution of a larval cestode, *Gilquinia squali*, in the eyes of whiting, indicated further subdivision of the northern stock into Scottish coastal, offshore and Shetland groups.

Recruitment migrations of North Sea herring

MacKenzie and Johnston (MS 1976) used the prevalences of three parasites (two nematodes and a cestode) to determine recruitment migrations of

TABLE 1. Summary of selected studies involving the use of parasites as natural tags (see note below Table).

Fish species	Geographic area	Parasite tags	Significant findings	Author(s)
Atlantic herring (*Clupea harengus*)	North Sea	*Anisakis* larvae (nematode)	Prevalence increased in 1966–68 and decreased in 1969-72, possibly due to change in migration behavior.	van Banning and Becker (1978)
	North Sea	*Lacistorhynchus* (cestode) *Renicola* (trematode metacercariae)	Distinguished juveniles of autumn-spawning herring populations from Bløden and Scottish coastal waters.	MacKenzie (MS 1974, 1975)
	North Sea	*Lacistorhynchus* (cestode) *Renicola* (trematode metacercariae)	Traced recruitment migrations of autumn-spawning herring in the North Sea and to the north and west of Scotland.	MacKenzie (MS 1975) MacKenzie and Johnson (MS 1976)
	North Sea	*Eimeria sardinae* and *E. clupearum* (coccidians)	Incidence of coccidians was found to be uniform, with no significant differences in various parts of North Sea and west coast of Scotland.	Kabata (1963a)
	Middle Atlantic coast of the United States	*Anisakis* larvae (nematode)	Lower levels of infestation in samples from Long Island to Chesapeake Bay than in areas to the North.	Lubieniecki (1973)
	Northwest Atlantic	*Anisakis* larvae (nematode)	Increase in prevalence with increasing latitude, Georges Bank fish having the lowest and Nova Scotia fish the highest prevalences.	Boyar and Perkins (MS 1971)
	Northwest Atlantic	*Anisakis* larvae (nematode)	Gulf of St. Lawrence/Southwest Newfoundland stocks probably do not intermingle with northeastern Nova Scotia stocks	Parsons and Hodder (1971)
	Northwest Atlantic	*Anisakis* larvae Trypanorhynch (cestode) larvae	Results show lack of intermingling of Gulf of St. Lawrence and Gulf of Maine fish.	Sindermann (1957a, 1957b, 1961)
Pacific herring (*Clupea pallasi*)	Alaska, British Columbia and Washington coastal waters	*Anisakis simplex* (nematode) *Thynnascaris adunca* (trematode)	Reliable separation of adjacent spawning stocks could not be accomplished.	Arthur and Arai (1980a, 1980b)
Sockeye salmon (*Oncorhynchus keta*)	North Pacific	*Triaenophorus crassus* (larval cestode)	Distinguished maturing and juvenile high seas salmon of Asiatic and North American origin	Margolis (MS 1956, 1963, 1965)
Atlantic salmon (*Salmo salar*)	North Atlantic	*Pomphorhynchus laevis* (acanthocephalan)	Parasite useful in indicating tributary of origin of salmon smolts in several Irish rivers, but utility in determining continent of origin of West Greenland high seas fish not established.	Pippy (1969a, 1969b)
	North Atlantic	*Anisakis simplex* (nematode)	Biochemical-genetic studies of nematode larvae indicated that different populations occur in widely separated N. Atlantic sampling sites.	Beverley-Burton *et al.* (1977) Beverley-Burton and Pippy (1977)
	Miramichi River New Brunswick	*Discocotyle sagittata* and *Diplostomum spathaceum* (trematodes) *Neoechinorhynchus rutili* (acanthocephalan)	Tributary of origin of smolts was indicated by parasite frequencies.	Hare and Burt (1975, 1976)

TABLE 1. (continued).

Fish species	Geographic area	Parasite tags	Significant findings	(Authors)
Whiting (*Merlangius merlangus*)	North Sea and British coastal waters	*Ceratomyxa arcuata* *Myxidium sphaericum* (myxosporidians)	Stocks of North Sea consist of distinct northern and southern populations, as do the stocks west of British Iles, but Irish Sea has a separate stock.	Kabata (MS 1959, 1963, 1967)
	Northern North Sea	*Gilquinia squali* (cestode)	Stocks could be separated into three distinct components — coastal, offshore and Shetland Islands.	Hislop and MacKenzie (1976)
Haddock (*Melanogrammus aeglefinus*)	North Sea and NE Atlantic	*Grillotia erinaceus* (cestode)	Several haddock subgroups were distinguished: two at Faroes, three to north and west of Scotland, and four in North Sea. Results showed a northward movement along the Scottish east coast.	Lubieniecki (1976, 1977)
Redfish (*Sebastes* sp.)	Northwest Atlantic	*Sphyrion lumpi* (copepod)	Major centers of infestation were off southern Labrador, SE slope of Grand Bank, and SE Gulf of St. Lawrence; the parasite was rare or absent elsewhere in sampling area.	Templeman and Squires (1960)
	Northwest Atlantic	*Sphyrion lumpi* (copepod)	High infestation in western Gulf of Maine but no infestation on southern Scotian Shelf, indicating absence of substantial intermixing.	Herrington *et al.* (1939) Perlmutter (1953)
	Northwest Atlantic	*Sphyrion lumpi* and *Chondracanthopsis nodosus* (copepods) *Anisakis* larvae Trypanorhynch larvae (cestode)	Each major redfish fishing area was discrete in terms of composite parasite frequencies, indicating absence of significant intermixing.	Sindermann (1963)
European plaice (*Pleuronectes platessa*)	Eastern North Sea	*Myxobolus aeglefini* (myxosporidian)	Parasite abundant in plaice from Skagerak but absent or rare in adjacent waters exploited by Dutch fishery.	van Banning *et al.* (MS 1978)
Atlantic cod (*Gadus morhua*)	Northwest Atlantic	*Lernaeocera branchialis* (copepod)	Parasite prevalence enabled identification of four subgroups: northern and southern Gulf of Maine, Georges Bank, southern New England.	Sherman and Wise (1961)
Baltic cod (*Gadus morhua callarias*)	Baltic Sea	*Anisakis simplex* and *Contracaecum aduncum* (larval nematodes)	Parasites differentiated three groups of Baltic cod, based on reciprocal prevalences of larval worms.	Grabda (1976)
Winter flounder (*Pseudopleuronectes americanus*)	Northwest Atlantic	*Glugea stephani*	Georges Bank population geographically isolated from fish on inshore grounds	Stunkard and Lux (1965)

Note: This table summarizes information for only 22 of several hundred studies of parasite tags for marine fish. A sampling of other relevant papers would include those by Davey (1972), Gibson (1972), Konovalov and Konovalov (1969), MacKenzie (1968), Olson and Pratt (1973), Platt (MS 1973), Scott (1969, 1975), Shotter (1973), and Shulman (1961).

autumn-spawning herring in the North Sea. Herring from the Minch showed changes with age consistent with continuous immigration from the Bløden grounds. The authors found, from parasite frequencies, that the proportion of immigrants increased from about 40% at age 2 to more than 80% in age 4+ herring.

Identification of the fishing zone of sole

An interesting case, in which the distribution of a parasite in a by-catch fish species was used to determine the fishing zone for a principal species, was reported by van Bannning *et al.* (MS 1978). To identify catches of sole, *Solea solea*, as coming from an area of the North Sea under quota regulation or from the free area of the Skagerak, parasites of plaice, *Pleuronectes platessa*, landed as by-catch with the sole, were examined. A protozoan parasite, *Myxobolus aeglefini*, was found to be highly prevalent in plaice from the Skagerak but very rare in plaice from the North Sea. The minimal intermixing of plaice substocks in the North Sea and adjacent waters was indicated by data collected during 1973–78.

Subgroups of Baltic cod

Prevalences of two larval anisakid nematodes, *Anisakis simplex* and *Contracaecum aduncum*, were used by Grabda (1976) to differentiate three groups of Baltic cod: those of the western Baltic (Pomeranian Bay and adjacent waters), those of the central Baltic, and those of the eastern Baltic. *Anisakis* prevalence decreased from west to east (zero in Gdansk Bay), whereas *Contracaecum* increased from west to east. The differential distribution of *Anisakis* was attributed to spawning migrations of heavily infested herring into the Baltic from western areas.

Categories of Parasite Tag Studies

The several studies noted above and others summarized in Table 1 can be categorized by types, generally in order of increasing complexity of the study. Four reasonably distinct types can be identified:

1. Surveys of prevalences of a simple parasite. (Examples are the redfish parasite *Sphyrion lumpi*, and the cod-gill parasite *Lernaeocera branchialis*.)
2. Surveys of two parasites, often with prevalences in two study areas. (Examples are the two North Sea whiting myxosporidans *Ceratomyxa arcuata* and *Myxidium sphaericum*, and the Baltic cod nematodes *Anisakis simplex* and *Contracaecum aduncum*.)
3. Surveys of parasite prevalences which are augmented by biochemical-serological, morphometric-meristic, age and growth, and artificial tagging studies. (Most parasite work is not done in a vacuum, because earlier indefinite information on populations and movements from other sources often exists. However, it is rare that other simultaneous studies are included in the experimental design of a parasite tag program.)
4. Surveys in which parasite frequencies in two host populations are not dissimilar, but population genetic differences exist in the geographic groups of parasites, detectable biochemically or immunologically. (One of the few examples of this type is found in the work of Beverley-Burton *et al.* (1977), in which acid phosphatase penotypes of larval *Anisakis simplex* varied in different sampling areas for Atlantic salmon and Atlantic herring, indicating the existence of more than one population of nematode larvae in the North Atlantic, because of the poor agreement of observed and expected enzyme phenotype frequencies, calculated according to the Hardy-Weinberg law.)

Case Histories

High seas migrations of Pacific salmon

From the data in Table 1, it is evident that parasite tags have been used extensively in studies of Pacific and Atlantic salmon. Some of the problems associated with biology and management of these anadromous species, for which parasites have provided useful data, include identification of the continent of origin and even the spawning areas of juveniles and maturing fish caught at sea, and identification of tributaries of origin of mixed stocks in downstream waters.

A major multinational investigation of geographic origins and migrations of Pacific salmon, particularly sockeye salmon, *Oncorhynchus nerka*, was conducted during the late 1950's. In studies which extended across the entire North Pacific Ocean, Margolis (MS 1956, 1963, 1965) demonstrated conclusively the extent of ocean migrations and the intermingling zone of salmon of North American and Asian origin. Using two freshwater parasites, the plerocercoid larvae of the cestode *Triaenophorus crassus* from the musculature and the adult nematode *Dacnitis truttae* from the intestine, he was able to draw specific conclusions which were substantiated by results of other studies. The larval tapework *T. crassus* was found in downstream migrant sockeye salmon only in some western Alaska river systems and was not acquired in the sea. The nematodes *D. truttae* occurred only in rivers on the coast of Kamchatka and was not found in North America. Maturing and immature sockeye salmon migrated up to 1,700 miles from Bristol Bay. An intermingling zone in the central North Pacific, where both parasites were found, was located between 170° W and 170° E. The prevalence of *T. crassus* in high seas samples of maturing fish and in samples of fish returning to spawn in Bristol Bay streams permitted estimates of the relative proportions of Bristol Bay salmon in the high seas fisheries.

This study, undoubtedly a classic of its genre, provided an early and robust demonstration of the utility of parasite tags.

Northwest Atlantic herring stocks

The distribution of herring in the western North Atlantic extends from Cape Hatteras to Greenland,

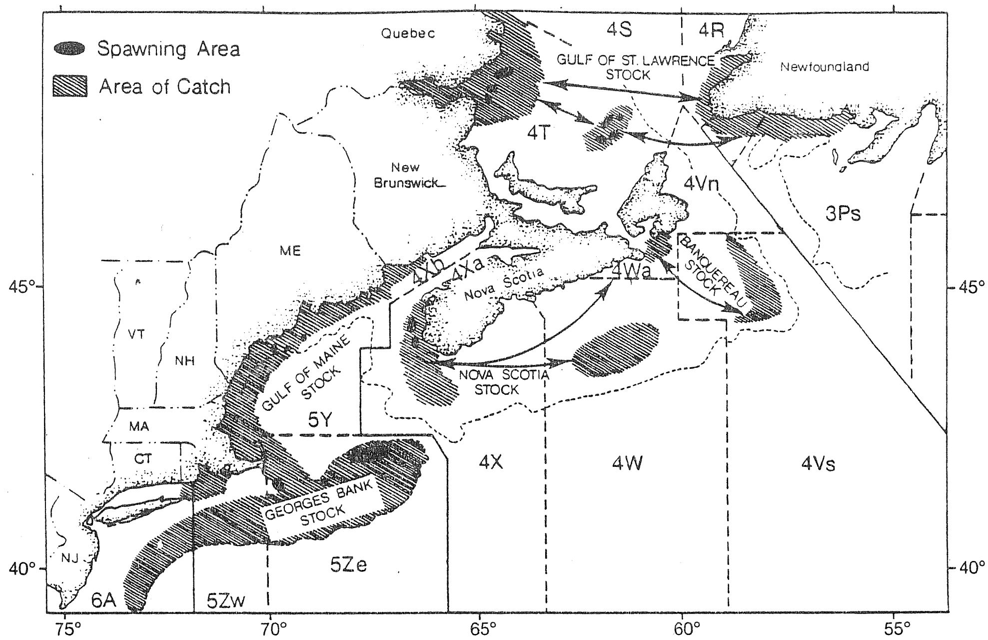

Fig. 1. Centers of herring abundance in the Northwest Atlantic (adapted from ICNAF, 1976, and redrawn from Anthony, 1977).

with a number of centers of abundance (so-called stocks or stock complexes). Those of the Gulf of St. Lawrence, Scotian Shelf, and Gulf of Maine including Georges Bank are shown in Fig. 1. The stocks can best be described at spawning time, because there is some evidence of intermixing and migrations at other times of the year. A variety of methods (morphometrics, meristics, age and growth studies, tagging, and biological tags) have been used for three decades to provide information about stock separation and movements of the various stocks, but some questions still remain.

Early studies of parasites of adult herring (Sindermann, 1957a, 1961) disclosed two encysted helminths, a trypanorhynchan cestode and an anisakid nematode, with geographic variation in abundance. The larval cestode was relatively abundant in Georges Bank and southern New England samples, rare in Nova Scotia samples and absent in the Gulf of St. Lawrence. Conversely, the larval nematode was much more abundant in Nova Scotia samples than in Georges Bank and southern New England samples, indicating only limited interchange between the two regions.

Subsequent studies of *Anisakis* larvae in herring (Boyar and Perkins, MS 1971, Hodder and Parsons 1971a, 1971b, Parsons and Hodder, 1971; Lubieniecki, 1973) have demonstrated its utility. Boyar and Perkins (MS 1971), from sampling during 1962–69, found that the nematode was at least twice as abundant in samples from Nova Scotia as in samples from Georges Bank and coastal Gulf of Maine, with infestation of Gulf of Maine fish being higher than on Georges Bank (Fig. 2). Lubieniecki (1973) found lower nematode incidences in samples from the Middle Atlantic Bight than those reported for more northern waters off Nova Scotia and Newfoundland. Parsons and Hodder (1971) found that the nematode was more abundant in samples from the Scotian Shelf than in those from southwestern Newfoundland and the southern Gulf of St. Lawrence. Similarities in nematode incidences between winter samples from southwestern Newfoundland and spring-autumn samples from the southern Gulf of St. Lawrence were considered to be supporting evidence that the fish form part of a single stock complex, as did similarities in incidences between northeastern Nova Scotia samples and those from the Banquereau-Cape Sable area.

Although there are persistent problems which are now being addressed by cooperative investigations by Canada and the United States, parasites have provided substantive information on stocks of adult herring.

In addition to these detailed and continuing studies of adult herring, parasites have provided information about movements of juvenile herring along the Maine coast. Two parasites, the myxosporidian *Kudoa clupeidae* which produces intramuscular cysts and the larval nematode *Anisakis* sp., have indicated very limited eastward movement of juveniles which had spent their first year of life on the western Maine coast, with possibly greater westward movement of fish which had spent their first year on the eastern Maine

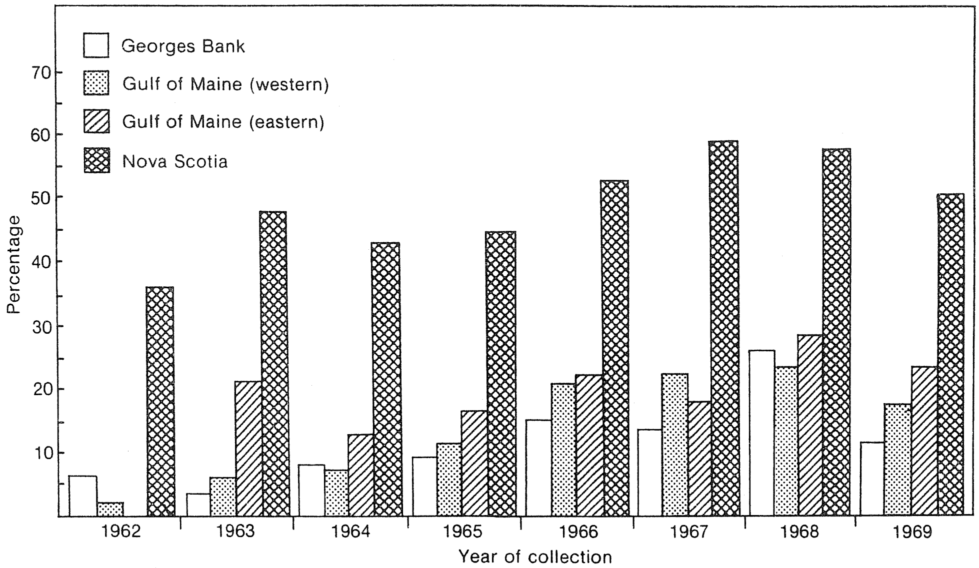

Fig. 2. Prevalence of the larval nematode, *Anisakis* sp., in the principal herring stocks of the Northwest Atlantic (redrawn from Boyar and Perkins, MS 1971).

coast (Sindermann, 1957a, 1957b). Subsequent tagging studies have also indicated limited movements of juveniles (Chenoweth *et al.*, MS 1980).

Conclusions

After three decades of research on the use of parasites as natural tags for marine fishes, conducted in the Atlantic and Pacific Oceans with a number of important commercial species, the utility of the method has been demonstrated adequately. Like any method of stock discrimination, the value of the approach is enhanced by simultaneous application of other methods, such as artificial tags, morphometric and meristic comparsions, age and growth studies, and biochemical-serological analyses. Parsite tags have particular value when the distribution and abundance of several different and persistent parasites can be studied over an extended period of time, and when concurrent life history and ecological studies can be conducted. Parasite data have often been of great value to the conclusions reached from studies based on more conventional approaches to stock discrimination.

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