



Contents lists available at ScienceDirect

# International Journal for Parasitology: Parasites and Wildlife

journal homepage: [www.elsevier.com/locate/ijppaw](http://www.elsevier.com/locate/ijppaw)

## Invited Review

# Parasites as biological tags to assess host population structure: Guidelines, recent genetic advances and comments on a holistic approach <sup>☆</sup>

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## ARTICLE INFO

### Article history:

Received 27 September 2013

Revised 21 November 2013

Accepted 21 November 2013

### Keywords:

Marine parasites

Host stock discrimination

Multidiscipline approach

Next-generation sequencing

Tag guidelines

Dicyemida

## ABSTRACT

We review the use of parasites as biological tags of marine fishes and cephalopods in host population structure studies. The majority of the work published has focused on marine fish and either single parasite species or more recently, whole parasite assemblages, as biological tags. There is representation of host organisms and parasites from a diverse range of taxonomic groups, although focus has primarily been on host species of commercial importance. In contrast, few studies have used parasites as tags to assess cephalopod population structure, even though records of parasites infecting cephalopods are well-documented. Squid species are the only cephalopod hosts for which parasites as biological tags have been applied, with anisakid nematode larvae and metacestodes being the parasite taxa most frequently used. Following a brief insight into the importance of accurate parasite identification, the population studies that have used parasites as biological tags for marine fishes and cephalopods are reviewed, including comments on the dicyemid mesozoans. The advancement of molecular genetic techniques is discussed in regards to the new ways parasite genetic data can be incorporated into population structure studies, alongside host population genetic analyses, followed by an update on the guidelines for selecting a parasite species as a reliable tag candidate. As multiple techniques and methods can be used to assess the population structure of marine organisms (e.g. artificial tags, phenotypic characters, biometrics, life history, genetics, otolith microchemistry and parasitological data), we conclude by commenting on a holistic approach to allow for a deeper insight into population structuring.

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## 1. Introduction

Determination of the biological identity of a population of marine organisms (for this review, limited to fishes and cephalopods), in relation to neighbouring populations of the same species, is a vital prerequisite in studying the biology, dynamics, interactions and ecological consequences of exploitation on that population (MacKenzie and Abaunza, 1998). This is particularly important given the rise in global fisheries as more species are being targeted and commercially exploited to keep up with increases in demand (Pierce and Guerra, 1994; Evans and Grainger, 2002). Marine species considered at risk as a result of overfishing, evident from declines in biomass and abundance, emphasise the importance of understanding the structure of populations across geographical distributions (Melendy et al., 2005; McClelland and Melendy, 2007). As alluded to already, before a stock can be efficiently managed and policies implemented for future sustainability, the stock needs to be correctly identified (Oliva and Sanchez, 2005).

Many techniques have been used to identify and discriminate stocks, including the application of artificial tags, such as acoustic tags, coded wire tags, passive integrated transponder tags and archival tags. Artificial tags are generally suitable for many species and sizes of organisms, with an added advantage of enabling discrete recognition of each tagged individual (Gillanders, 2009). However, they can be limited in signal detection range and retention over long term studies, with further uncertainties about the influence of the tag on the organism's behaviour and survivorship (Moser, 1991; Mosquera et al., 2003; Gillanders, 2009). Natural tags, including phenotypic characters (meristic, morphometric and life history traits), otolith chemistry, molecular genetic host markers and parasites, have also been used in population structure studies. In particular, parasites as biological tags have gained wide acceptance in recent decades (MacKenzie, 2002; Poulin and Kamiya, in press), as they can provide a reliable guide to understanding the biology of their host (Pascual and Hochberg, 1996). This is not to say parasites as tags are superior to other methods, but it is recognised that they have helped answer questions on host diet and feeding behaviour, movements and ranges, connectivity of stocks, recruitment patterns of juveniles and phylogenies (Sindermann, 1961; Moser, 1991; Williams et al., 1992; Criscione et al., 2006). Parasites have also been used as bio-indicators of pollution (Poulin, 1992; MacKenzie et al., 1995; MacKenzie, 1999a), and in population studies to discriminate stocks (MacKenzie, 1987, 2002; Lester, 1990; MacKenzie and Abaunza, 1998; Mosquera et al., 2003). Research on parasites as biological tags for marine organisms has increased at a steady rate, with nine papers on this subject published from the 1950s, more than 30 from the 1960s, more than 50 from the 1970s and more than 140 from the 1980s (Williams et al., 1992). Here, we focus on the use of parasites as biological tags for host population discrimination. We use the words 'stock' and 'population' interchangeably in this review, following the definition provided by Charters et al. (2010) of 'a spatially distinct group of marine organisms which exhibit no significant mixing with neighbouring individuals'. In agreement with Lester and MacKenzie (2009), we recognise the idea that this distinct group is essentially self-reproducing.

This review begins by briefly commenting on the importance of accurate parasite identification, followed by a summary of the use of parasites as biological tags in population structure studies of fishes and cephalopods. Due to the advent of molecular genetic technologies, the potential to incorporate genetic analyses of parasite population structure alongside genetic analyses of their host is discussed. An updated list of guidelines for selecting a parasite species as an adequate tag candidate is presented, and we conclude by highlighting the benefits of a multidisciplinary

approach when investigating the population structure of marine organisms.

## 2. Parasite identification

Along with the need to correctly identify a stock before it can be appropriately managed, parasites also need to be correctly identified before they can be applied as biological tags. We add the caveat that in some cases the minimum necessary identification would be to discriminate each of the parasite species present without the further and potentially time consuming requirement of assigning scientific names. Classical methods commonly used for parasite taxonomic identification involve examining and measuring morphological character traits and using taxonomic keys to define a particular family, genus or species (Baldwin et al., 2012). Although widely used and relatively inexpensive, this form of identification can be difficult for larval stages and further hindered by poor specimen quality and taxonomic uncertainty in the literature. "Species" that exhibit a high level of morphological plasticity also pose a problem (Poulin and Morand, 2000). On one hand, several distinct species may be mistakenly identified as one, or a single morphologically plastic taxon may be interpreted as a species complex inferring significant host population structure.

Another approach to identify parasite species is to use molecular genetic methods (McManus and Bowles, 1996). Indeed, once a sound molecular genetic framework has been established for the species concerned, then higher throughput bar-coding can be applied to much larger sample sets. Another advantage of this approach would be that all stages of the parasite life cycle that could be sampled can be included, potentially increasing the matching parasite data for a larger number of host individuals collected over a longer period of the year. A combination of morphological and molecular genetic methods may therefore be more robust for identifying and discriminating parasite taxa, and should be considered in future studies using parasites as biological tags.

## 3. Parasites as biological tags in population studies of fishes

The two earliest records describing the application of parasites as biological tags in population studies of fishes are that of Dogiel and Bychovsky (1939), who distinguished between groups of sturgeon (*Acipenser* spp.) in the Caspian Sea using the monogenean parasites *Diclybothrium circularis* and *Nitzschia sturionis*, and Herrington et al. (1939), who examined redbfish (*Sebastes marinus*) in the Gulf of Maine and suggested the existence of separate populations based on variations in infection levels of the parasitic copepod *Sphyrion lumpi*. Since these investigations over 70 years ago, the use of parasites as biological tags in population structure studies has flourished to include a wide range of fish species and geographical localities. Investigations have primarily focused on, although not limited to, fish species of economic importance, such as herring (e.g. Sindermann, 1961; Parsons and Hodder, 1971; Arthur and Arai, 1980; Moser and Hsieh, 1992), hake (e.g. MacKenzie and Longshaw, 1995; George-Nascimento, 1996; Mattiucci et al., 2004; Sardella and Timi, 2004), cod (e.g. Hemmingsen and MacKenzie, 2001; McClelland and Melendy, 2011), rockfish (e.g. Stanley et al., 1992; Moles et al., 1998; Oliva and Gonzalez, 2004) and hoki (e.g. MacKenzie et al., 2013). A diverse range of taxonomic groups of parasites have also been applied as biological tags (see Table 1 in Williams et al., 1992). In particular, parasites have been used for discovering multiple species in supposedly single species fisheries (e.g. Smith et al., 1981; George-Nascimento, 1996), for discriminating stocks within single species fisheries (e.g. Hemmingsen et al., 1991; Braicovich and Timi, 2008; Henriquez et al., 2011) and for

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