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REVIEWS

Integrating fish and parasite data as a holistic solution for identifying the elusive stock structure of Pacific sardines (*Sardinops sagax*)

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Abstract There is an urgent need to clarify how different stocks, or subpopulations of fish species, are vulnerable to fishing pressure and unfavorable ocean conditions because of the increasing demand on fisheries for human consumption. For marine fishes, the potential for high gene flow increases the difficulty in determining the number of subpopulations managed in a specific fishery. Although the use of molecular data has become a common method in the past 15 years to identify fish subpopulations, no single technique or suite of techniques has been established for fish stock structure studies. We review the use of fish morphometrics, artificial tags, fish genetics, parasite genetics, and parasites as biological tags to identify subpopulations of marine fishes with a focus on the Pacific sardine (*Sardinops sagax*) fishery off the west coast of North America. We suggest an integration of fish- and parasite-based techniques for future stock structure studies, particularly for pelagic fish species whose stock structure can be elusive. An integration of techniques may also resolve fish stock structure over small geographic areas by increasing the number of spatial and temporal scales studied simultaneously leading to methods for successful management of marine fish species.

Keywords Pacific sardine · Fish stock identity · Fisheries · Parasite biological tag

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Introduction

An estimated 81.9 million tons of marine fish were captured in 2006 by the world's fisheries (FAO 2008). This demand for fish is predicted to continue increasing along with the human population, which is expected to reach over 9 billion by 2050 (Ryman et al. 1995; Waples 1998; WGBH Educational Foundation 2004). With approximately 50% of the world's marine stocks currently considered over-exploited (FAO 2008), the sustainability of harvesting marine fish populations is in doubt. Early in the twentieth century, fish stock models were developed to calculate marine fish stock biomass available to harvest each year while still

maintaining viably productive populations (Beverton 2002). Five of the earliest mathematical models used to estimate fish population biomass yields were: the length-based yield biomass equation (Baranov 1918), a simple logistic production curve to estimate maximum yield (Graham 1935), a physiological growth curve (von Bertalanffy 1938), a maximum yield versus recruitment curve (Ricker 1954), and a constant population recruitment model (Beverton and Holt 1957). Most fish harvest guidelines have been established based on these and more recent models (Quinn and Deriso 1999) that may include sustainability (Quinn and Collie 2005), migration in a catch-age analysis (Quinn et al. 1990), target species in relation to predation (Hollowed et al. 2000) or their prey (Collie and Gislason 2001), multi-species interactions and their responses to changing environmental conditions (Mace 2001) like the models Ecopath, Ecosim, and Ecospace (Pauly et al. 2000; Olson et al. 2005), and more recently EcoTroph (Gascuel et al. 2009) that replaces the parameter time with trophic level; however, evidence continues to indicate that many fish populations are over-exploited (Pauly et al. 2000).

Models are only as good as the data used to create them (Beverton 1998), and problems with yield models are in part due to the difficulty identifying and assessing interactions among all the components of each fishery (Smith 1998; Schnute and Richards 2001). For instance, earlier models did not necessarily account for fish recruitment failures (Beverton 1998), the boom and bust nature of forage fish species (Alder et al. 2008), or the accidental mixing of fish populations in fishery data, which made it difficult to later separate fish into distinct groups (Sinclair and Solemdal 1988). In addition, fisheries models published from 1948 to 1977 were created during a period with relatively stable ocean conditions compared to today (Mantua et al. 1997; Peterson and Schwing 2003). Important theories of fisheries management may have differed if these early models had been able to incorporate oceanographic conditions, since the same model relationships may not be appropriate for use in different regimes or states of the ocean (Beamish et al. 2000).

Fish react to changes in their environment (physical and biological); however, single-species models may be too simple to capture the vicissitudes of complex ecosystems (Smith 1998). Changes in a fish population size via birth, individual movement, and death are often not well captured by abstract representations in a fisheries model, thus mathematical values become disconnected from the fish life-history characteristics they represent (Rose 1997; Beverton 1998; Schnute and Richards 2001). Further, one fishery model may not apply to different populations of the same fish species (Schnute and Richards 2001; Longhurst 2006), since it is unclear how fishing affects the ability of each population to overcome recruitment failures due to adverse environmental conditions (Mann 2000). It is also unclear if fish that are commercially exploited sustain sufficient rigor to withstand fluctuating ocean conditions as they would have done prior to exploitation (Mann 2000). Thus, model shortcomings and data uncertainty, in combination with inevitable fluxes in environmental conditions, limit the value of using past data to define the future status of a specific fish population or species (Schnute and Richards 2001, Caddy and Seijo 2005).

The stock concept was introduced to better understand the vulnerability of subpopulations within specific species to over-fishing, and to help delineate which fishing areas and components were most at risk of being over-fished. A stock can be defined as a group of individuals of a particular species whose genetic characteristics, and usually life history characteristics, are more similar to each other than other stocks (Waldman 2005). Stock identification of economically important fish species is needed to determine boundaries of specific populations of a species (Waldman 2005), what regulates subpopulation abundance, reproduction, growth, and survival (Grant and Bowen 1998). If stocks can be identified, then it is possible to understand how or why a fishery might exploit specific components of a population (Waples 1998). Marine fish stock identification has been challenging, since relatively few barriers exist in the marine environment that might delineate dispersal and migration compared to those in terrestrial or freshwater environments (Waples 1998). Knowing the identity of a stock is especially important for highly migratory fish species that cross state or country boundaries because changes in their distributions can result in changes to harvest availability in various state, national or international political jurisdictions. Stocks can also be considered a construct between a fish species and the current management strategy for that fishery. Thus identifying the subpopulation composition of a fish stock and the boundaries between stocks are critical in providing

a biological understanding of stocks to fisheries management; especially if the current stock structure opposes historically established stock and management boundaries (Begg and Waldman 1999), and are not based on natural phenomena that are perpetuated through time (Sinclair 1988; Abaunza et al. 2008b). Most information on stock identification has been collected by applying morphological characteristics, artificial tags, biological tags, and genetic techniques (Cadrin et al. 2005).

During the 1930s the Pacific sardine (*Sardinops sagax*) fishery was considered the largest in the Western Hemisphere (Wolf 1992), contributing almost 25% of the total fish landed in the United States (McEvoy and Scheiber 1984). Tagging studies in the 1930s and 1940s suggested that Pacific sardine caught in the California Current from British Columbia, Canada, to southern California were one stock (Janssen 1938; Clark and Janssen 1945). Evidence indicated that after spawning off southern California in spring, the larger sardines migrated north to feeding grounds off of the Columbia River and into Canadian waters. At the onset of winter storms, sardines then migrated back to southern California to overwinter (Marr 1957, 1960). The coastwide fishery began to collapse in the 1940s, with closures off British Columbia in 1947 and off of central California in 1967 (Radovich 1982).

By 1992 sardines re-appeared in large numbers in the Pacific Northwest (PNW; Oregon, Washington, and British Columbia, Canada) (Hargreaves et al. 1994). However, it remains uncertain whether the coastwide migration pattern described prior to the fisheries collapse of the 1940s has resumed, or whether there are sub-populations of sardine along the coast with limited migration among smaller groups. Successful sardine recruitment has been observed off the Columbia River (Bentley et al. 1996, Emmett et al. 2005) lending support for a separate stock in the PNW, but sardine genetic data have been inconclusive in identifying more than one stock between California and British Columbia (Hedgecock et al. 1989; Lecomte et al. 2004; J. Hyde pers. comm.). If more than one stock exists in this part of the California Current, understanding the connections between potential sub-populations has important management implications, since sardine fisheries in the United States and Canada are currently managed as one stock (latest stock assessment by Hill et al. 2010).

Biological tags such as trophically transmitted parasites have been used to assess migration patterns and stock identity of their fish hosts (see review by MacKenzie 2002), but parasites have yet to be included in an assessment for Pacific sardine. Our objectives for this review are to describe different methods used to assess fish stock identity of Pacific sardines, review the success of using parasites to examine fish stock identity, and affirm the merits of an holistic approach whereby a variety of biological data from the same individual fish are gathered (Begg and Waldman 1999) including fish data and parasite data (both community and genetic) to resolve more challenging stock identification scenarios like Pacific sardine.

Fish stock identifications: morphology and artificial tags

The California Current Pacific sardine is an economically and ecologically important fish whose stock identity has been assessed using several different approaches (Smith 2005). Early sardine studies compared the variation in morphology (or meristics) between individual fish. Clark (1947) and Wisner (1960) suggested that sardine populations could be separated based on vertebrae number. Sardines from more northern latitudes (such as the PNW) had more vertebrae on average than sardines from southern latitudes (such as southern California and the Gulf of California). Clark (1947) suggested that the development of more vertebrae resulted from colder ocean temperatures during development, and that individuals could be traced to their source population by assessing vertebrae number. Other sardine meristic studies have included size at age determined by scales and otoliths (Felin 1954), blood groups (Sprague and Vrooman 1962), otolith morphometry (Félix-Uraga et al. 2005), and otolith microchemistry (Jones 2006).

Although fish are often collected opportunistically, within the geographical range of a species (Jones 2006), there has been some success in identifying different stocks of Pacific sardine on a large geographic scale (Smith 2005). Recently, Félix-Uraga et al. (2004) developed a temperature distribution model that identified Pacific sardine groups from southern California to the Gulf of California. The

following three groups were based on time of year and specific ranges in sea surface temperatures: (1) 13–17°C (cold water group) from San Pedro, California, to Ensenada, Baja, California; (2) 17–22°C (temperate water group) from Ensenada, Baja, California to Magdalena Bay, Baja, California; and (3) 22–27°C (warm water group) from Magdalena Bay, Baja, California, to the Gulf of California. Radovich (1962, 1982) suggested a far northern stock existed in the California Current from Point Conception, California, to British Columbia, Canada, prior to the westcoast fishery collapse. However, only three Pacific sardine stocks are currently recognized: (1) Central California offshore; (2) Baja California Sur inshore; and (3) Gulf of California (Smith 2005).

Mark-recapture studies provide insight into fish migration patterns (Jakobsson 1970; Hansen and Jacobsen 2003; Orbesen et al. 2008), spatial separation of stocks (McFarlane et al. 1990; Neilson et al. 2006; Armannsson et al. 2007), and estimates of the proportion of individuals intermingling among stocks (Teel et al. 2003; Hoenig et al. 2008). Early sardine migration studies used metal tags attached to the operculum or caudal fin, or inserted into the abdominal cavity (commonly known as "belly tags"; Rounsefell and Dahlgren 1933). When the electromagnetic tag-detection technology enabled an individual tag to be associated with a specific fish, belly tags became the preferred tagging method for pelagic fishes (Dahlgren 1936; Hart 1943; Ahlstrom 1957). Based on meristic and tagging studies, Marr (1957) concluded that Pacific sardine migrated back and forth between southern California and the Pacific Northwest. Further tagging research by Marr (1960) showed that the northward migration of Pacific sardine extended to Vancouver Island, British Columbia. This supported Clark's (1935) hypothesis that in the Northern California Current, Pacific sardine were one continuous population.

Attempts to repeat these early tagging studies for Pacific sardine have been difficult. High rates of tagging mortality are expected, since in tagging studies conducted between 1936 and 1942 (Clark and Janssen 1945), up to 80% of small fish (<185 mm in total length), and 70% of large fish (>185 mm in total length) died before or shortly after release. In general smaller fish have been more prone to complications related to scale loss (Harrt 1963; Hansen and Jacobsen 2003), which may explain the excessive mortality described by Janssen and Alpen (1945), after using belly tags in Pacific sardines smaller than 140 mm in total length. Clark and Janssen (1945) observed increasing mortality rates with prolonged fish handling and holding fish in captivity, and currently there are limited facilities available to hold sardines with minimal mortality.

Thousands of tagged fish are needed to increase the probability of future recovery (Jacobson and Hansen 2005), hence costs also need to be considered. Coded-wire tags cost $0.15 each (Johnson 2004) compared to $20 each for electronic tag with temperature recording capabilities (Welch et al. 2003). Electronic tags are larger than coded wire tags; thereby their use is restricted to larger fish. Thus, with cost restrictions and expectations of high mortality rates, it is unlikely that a large-scale mark-recapture program will be initiated soon for Pacific sardine. Nevertheless, such a program would be required to assess whether migration patterns observed more than 60 years ago have resumed under current ocean conditions.

Fish stock identification: molecular markers

Technological advances over the past 25 years have enabled detailed examination of genetic material, and for the past 15 years, molecular markers have become the most favored method to assess fish population stock identity. Fishery scientists have used many different types of genetic markers, including allozymes (Waples et al. 2008), mitochondrial DNA (mtDNA) (Waples et al. 2008), microsatellite loci (Hedrick 1999), and single nucleotide polymorphisms (SNPs, Morin et al. 2004). All four types of genetic markers are still in use today, providing opportunities to analyze fish stock structure over various time and spatial scales.

Allozymes, allelic forms of a protein (King and Stansfield 1985), were among the first genetic markers applied to the study of animals (Harris 1966; Hubby and Lewontin 1966; Lewontin and Hubby 1966). These markers have a low mutation rate (10^{-7} mutations per generation; Nei 1987) and provide a qualitative description for specific Mendelian loci (Avise 1998). Hedgecock et al. (1989) used 32 allozyme loci to examine Pacific sardine collected from central California to the Gulf of California. Genetic variation was low, with rare alleles shared

among distant locations; thus, sardines were considered one population (Hedgecock et al. 1989). In contrast, semi-isolated groups of European sardine (*Sardina pilchardus*) from the western Mediterranean Sea were described using 15 loci, with fish collected off Alboran considered distinct from the remaining geographic locations (Ramon and Castro 1997). Recently, allozyme data indicated a weak population structure for the European sardine in the Atlantic Ocean, where samples from the Azores, Mauritania, and Maderia were distinct from those of coastal Europe and northwest Africa (Laurent et al. 2007). In particular the super-oxidase dismutase (SOD*) locus was associated with genetic differences between geographic locations (Laurent et al. 2007). This pattern had been previously observed by Chlaida et al. (2006), whose study focused on sardine populations off Morocco. Although sardine populations can be identified using allozymes, they comprise less than 1% of the total genome (Nei 1987) and require reproductive isolation among contributing subpopulations for several generations before genetic differences can accumulate (Koljonen and Wilmot 2005).

Mitochondrial DNA (mtDNA) is a haploid genetic marker that characterizes matrilineages within and among species (Avise 1998). Mitochondrial DNA markers are well represented in most genomes, have a high copy number (Allendorf and Luikart 2007), and have regions with varying mutation rates (10^{-1} to 10^{-3} mutations per generation). These mtDNA markers have mutation rates five to ten times faster than those estimated for some nuclear DNA (Brown 1983). Discrete stocks of marine fish have been defined using mtDNA, such as thornyheaded rockfish (*Sebastolobus alascanus*) (Stepien 1995) and blue rockfish (*Sebastes mystinus*) (Cope 2004). However, geographically separated populations have not been identified for either Pacific sardine in the California Current (Lecomte et al. 2004), or European sardine off Turkey (Sarmaşik et al. 2008). Evidence of a genetic bottleneck for European sardines caught off Safi, Morocco, was described using a 387 base pair (bp) portion of the mtDNA control region, but no other populations were identified for the Atlantic Ocean and Mediterranean Sea (Atarhouch et al. 2006). Historical divergences (over the last few million years) between populations or stocks can be detected using mtDNA, but these markers may fail to detect more recent divergences (within the last ten thousand years) (Hewitt 2004). Additionally it is impossible to resolve hybrid matings with a maternally inherited marker. Thus, mtDNA may be inappropriate for stock identification among recently diverged subpopulations, or for fish species like sardines, which have expanding and contracting population dynamics.

Microsatellites are repetitive sequences of DNA, usually two to four nucleotides long (e.g., AC or GATA), and often in assemblages ranging from five to 50 repetitions (Dewoody and Avise 2000). Microsatellites are co-dominant markers widely dispersed along and among chromosomes, with each locus defined by a specific DNA sequence. With 10^{-4} to 10^{-5} mutations per generation (Bruford and Wayne 1993), the mutation rate of microsatellites is high compared to that of allozymes. Sometimes unique alleles are observed for localized populations, but more often, differences in allele frequencies are used to separate populations. For instance, Beacham et al. (2008) used 14 microsatellite loci to confirm that four stocks of Pacific herring (*Clupea pallasi*) in British Columbia, Canada, were distinct from each other as well as from herring stocks from southeast Alaska, Washington, and California. Eight microsatellite loci were used to identify a weak genetic structure for European sardines in pairwise comparisons between populations from the Central Atlantic Ocean and the Mediterranean Sea. However, no geographically distinct populations were detected among those stocks (Gonzalez and Zardoya 2007). So far, eleven microsatellites have been reported for Pacific sardine (Pereyra et al. 2004), with data providing generally weak support for separate regional stocks; however, some cases of adjacent samples have appeared more distinct than samples collected at opposite ends of the California Current (J. Hyde pers. comm.).

The newest molecular markers assessed for stock identification are single nucleotide polymorphisms (SNPs) (Vignal et al. 2001; Morin et al. 2004), which are nucleotide sites with single nucleotide differences between alleles (Smith and Seeb 2008). Typically SNPs only have two alleles per marker (bi-allelic) and have been found in roughly every 200–500 base pairs throughout the genome in coding and non-coding regions (Morin et al. 2004). Smith and Seeb (2008) suggested that SNPs had some concordance

with microsatellites and allozymes in separating eleven chum salmon (*Oncorhynchus keta*) populations into seven reporting groups. Morin et al. (2004) suggest that several SNP loci exist in a more representative sample of the entire genome and have less sampling variance than microsatellite loci. More SNP loci are required to produce statistical power similar to that of microsatellite loci, and currently no information is available on the SNPs in sardines. Therefore, without a priori knowledge of the expected genetic variability in a fish species, SNPs may not be the best choice for a population genetics study.

With the ongoing development of new molecular markers and increasing availability of genetic sequences, identifying individual fish to specific populations or stocks has become possible with different assignment methods (Hansen et al. 2001; Manel et al. 2005). Assignment tests may be used to categorize individuals of unknown origin to a specific population or stock that has been determined a priori (Manel et al. 2005). For instance, Narum et al. (2008) used both microsatellites and SNPs to differentiate 29 populations (>99% of pairwise tests) of Chinook salmon (*O. tshawytscha*) from the Pacific coast of North America; however, the 13 microsatellites had better resolution for separating closely related populations than the 37 SNPs applied in that study. Using data from eight microsatellites Gonzalez and Zardoya (2007) correctly assigned only 20.1% of individual European sardines to their source population, in part due to the difficulty in clarifying the number of source populations in the central Atlantic Ocean and the Mediterranean Sea. Instead of assigning individual fish, population differentiation assigns a proportion of individuals to a specific population of origin. Using nine microsatellite loci, Ruzzante et al. (2010) documented three spawning groups of Atlantic herring (*C. harengus harengus* L.) located in the North Sea, the Skagerrak, and from the Kattegat and Western Baltic despite evidence for mixing in nursery, feeding, and overwintering aggregations. To date, population differentiation has not been attempted for sardines. As for individual molecular markers, the power of assignment methods depend on the markers used, the number of loci and fish sampled, and the level of differentiation that exists between pre-determined populations (Manel et al. 2005).

Recommendations on fish molecular markers

Hedgecock et al. (1989) speculated that Pacific sardine has less genetic diversity than other clupeid fish species. Genetic information may be contributed by few founder individuals, since Pacific sardine is frequently absent from the California Current as measured by scale deposits in anaerobic sediments (Soutar and Isaacs 1969; Baumgartner et. al 1992). Also, Pacific sardine may be a recent colonizer of the California Current compared to other pelagic fish. Sardine fossil remains are absent in sediments from the Pliocene and Pleistocene, when other pelagic fish species were present (Fitch 1969). When molecular markers are included in future stock assessments of Pacific sardine, the interpretation of population structure may differ depending on the type of marker used, the number of loci examined, and the geographical scope of populations included in the analysis. For example, Buonaccorsi et al. (2001) observed interspecific genetic differences for blue marlin (*Makaira nigricans*) caught in either the Atlantic or Pacific Ocean, using allozymes, mtDNA, or five microsatellite loci. Even though almost 43% of all Atlantic samples comprised one of two clades, intraspecific population structure was difficult to detect. Interannual variability among locations (particularly for blue marlin caught off of Hawaii) was observed only using mtDNA, and a significant divergence among individual fish was suggested only by microsatellite loci. Microsatellite and mtDNA were more divergent and variable than allozymes, but there was no consistent support among the molecular markers for either higher or lower diversity in either the Atlantic or Pacific Ocean (Buonaccorsi et al. 2001). Grant and Utter (1984) suggested that allozymes may be insensitive to populations of Pacific herring (*C. pallasi*) that had recently been genetically separated. They further cautioned the use of any molecular markers for a forage fish species whose population size can expand and contract over decades. Furthermore, difficulty remains in resolving stock identity over relatively small geographic distances in the marine environment, where evidence for high rates of gene flow remains common, regardless of the type of molecular marker applied (Hedgecock 1986; Lessios et al. 1998; Smith and Seeb 2008; Nielsen et al. 2009a, b). We thus consider hereafter the potential of other methods for complimenting fish

genetic data, since data generated using molecular approaches have yet to definitely resolve the identity of different stock groups of Pacific sardine in the California Current.

Fish stock identification: parasites

Using parasite species as biological tags is another approach applied to identify fish population stock identity (see review by MacKenzie 2002). Parasites are naturally acquired by their fish hosts, and can provide ecological information on nursery grounds, migration, and foraging history (Thomas et al. 1996). Parasites infect fish directly by attachment or penetration, or indirectly through consumption of infected prey (Marcogliese 1995; Rhode 1984). Once a fish is infected, parasites can remain in or on the host for months to years depending on longevity of the parasite species and other aspects of the host-parasite association (Rohde 1984). The total variation in the number of parasite species recovered (community diversity), the percentage of fish infected (prevalence), the number of parasites per fish host (abundance), and the number of parasites per infected fish host (intensity) (Bush et al. 1997) have been used to discriminate between fish stocks (Lester 1990; Thomas et al. 1996; MacKenzie and Abaunza 1998).

There is a long history of applying parasites to delineate stocks of marine fish (Table 1). An early study by Herrington et al. (Herrington et al. 1939) used the presence of the parasitic copepod (*Sphyrion lumpi*) to separate two stocks of redfish (*Sebastes marinus*) harvested off the Atlantic coast of the United States. Since that time, parasites (either single or multiple species) have been used to identify stocks of marine fish worldwide (Table 1; MacKenzie and Abaunza 1998; Mattiucci 2006).

The following characteristics are important in choosing a parasite species as a biological tag: (1) infection should not result in selective mortality; (2) the parasite is easy to recover and identify; (3) there is variation in parasite abundance between geographic locations; (4) individual parasites remain in or on a host for several months to years; and (5) the parasite is host specific (MacKenzie and Abaunza 1998; Bush et al. 1997; MacKenzie 2002). Host specificity may not be as stringent a requirement for marine parasite species compared to the other characteristics, since parasite generalists are more common among marine hosts (Marcogliese 2002). Generalist parasites have the ability to infect several different host species, are often transmitted by several different pathways in marine food webs, and are frequently observed when host distribution is patchy (Marcogliese 1995, 2002). For example, approximately 200 host species (both invertebrates and vertebrates) are known to exist in the northern latitudes for the nematode *Anisakis simplex sensu stricto* (Cross et al. 2007). Cross et al. (2007) advocated that *A. simplex s.s.* is a valuable biological tag, since it had temporal stability throughout the year and thus could be maintained within a specific geographical area over time. Although several related host species or taxa increase the complexity of a parasite life cycle, this may in fact increase the probability for transmission when large geographic scales reduce encounter rates between first and final host (Marcogliese 1995; Nadler 1995).

While one parasite species can be used to discriminate between different host populations, in reality, individual hosts are often infected with more than one parasite species at any given time. By examining parasite communities, host populations could be further subdivided over several spatial and time scales (Nadler 1995; Marcogliese et al. 2003; Mattiucci et al. 2004; McClelland et al. 2005; Criscione et al. 2006). For instance, fish stocks of the western group of deepwater redfish (*Sebastes marinus*) within the Gulf of St. Lawrence and Newfoundland were initially identified using fish molecular markers (Roques et al. 2002) and were further subdivided into four smaller groups using three parasite species (Marcogliese et al. 2003). Also, the fish groups defined by parasite community analysis supported the current stock boundaries previously defined by fisheries managers (Marcogliese et al. 2003).

For Pacific sardine of the Central California Offshore stock, there is evidence of two separate yet overlapping migration routes in the California Current System based on the distributional patterns of two trematode species. The previously described coastwide migration pattern from southern California to Vancouver Island, British Columbia (Janssen 1938; Clark and Janssen 1945) is supported by the distribution of the trematode *Myosaccium ecaude* (Baldwin 2010 Ph.D. dissertation), known to only infect Pacific sardine (Montgomery 1957). A second migration

Table 1 Examples of macroparasite biological tag studies that have been conducted for a variety of marine and anadromous fish species since 1939

Year	Fish species	Parasite species	Study location	References
1939	Redfish (*Sebastes marinus*)	Copepoda (*Sphyrion lumpi*)	Western Atlantic Ocean	Herrington et al. (1939)
1963	Sockeye Salmon (*Oncorhynchus nerka*)	Cestoda (*Triaenophorus crassus*) and Nematoda (*Dacnitis truttae*)	North Pacific Ocean	Margolis (1963)
1981	Arctic Char (*Salvelinus alpinus*)	Cestoda (*Diphyllobothrium* spp., *Eubothrium salvenlini*, *Proteocephalus longicollis*), and Trematoda (*Brachyphallus crenatus*, *Bothrimonus sturionis*, and *Prosorhynchus squamatus*)	Canada	Dick and Belosevic (1981)
1984	Steelhead (*Salmo gairdneri*)	Trematoda (*Plagioporus shawi* and *Nanophyetus salmonicola*)	North Pacific Ocean	Margolis (1984)
1985	Atlantic Herring (*Clupea harengus*)	Larval Nematoda (*Anisakis simplex* and *Hysterothylacium aduncum*), and Trematoda Metacercariae (*Cryptocotyle lingua*)	Northwestern Atlantic Ocean	McGladdery and Burt (1985)
1985	Herring (*C. harengus*)	Metacercariae Trematoda (*Cercaria pythionike* and *C. doricha*), and plerocercus Cestoda (*Lacistorhynchus* sp.)	North Sea, North and West of Scotland	MacKenzie (1985)
1985	Skipjack Tuna (*Katsuwonus pelamis*)	Didymozoid Trematoda (*Didymocylindrus filiformis*, *D. simplex*, *Didymoproblema fusiforme*, *Lobatozoum multisacculatum*, *Coeliodidmyocystis* sp., *Oesophagocystis dissimilis*, *Kollikeria*/*Didymocystis* spp., *Didymocystoides intestinomuscularis*, and *Lagenocystis*/*Univitellannulocystis* spp.)	New Zealand	Lester et al. (1985)
1988	Orange Roughy (*Hoplostethus atlanticus*)	Larval Cestoda (*Callitetrarhynchus* sp. and *Hepatoxylon trichiuri*), and Larval Nematoda (unidentified Spirurid, *Anisakis* sp. type 1, 2, and 3, *Terranova* sp.)	Australia, New Zealand and Tasmania	Lester et al. (1988)
1992	Pacific Herring (*C. h. pallasi*)	Cestoda (*Lacistorhynchus dollfusi*), Trematoda (*Parahemiurus merus*), Nematoda (*A. simplex*, *Hysterothylacium* sp. and *Contracaecum* sp.)	Central California	Moser and Hsieh (1992)
1992	Yellowtail Rockfish (*S. flavidus*)	Monogenea (*Microcotyle sebastis*)	Pacific Coast off North America	Stanley et al. (1992)
1993	Greenland Halibut (*Reinhardtius hippoglossoides*)	Acanthocephala (*Corynosoma strumosum*), Larval Nematoda (*A. simplex*, *Psuedoterranova decipiens*, Contracaecienea), Trematoda Metacercariae (*Otodistomum* sp.)	Canadian Northwest Atlantic	Arthur and Albert (1993)

Table 1 continued

Year	Fish species	Parasite species	Study location	References
1993	Hake (*Merluccius capensis* and *M. paradoxus*)	Monogenea (*Anthocotyle merluccii*), Larval Cestoda (*Clestobothrium crassiciceps*, *Scolex pleuronectis* and *Leptotheca* spec.) Copepoda (*Brachiella merluccii*), Larval Nematoda (*Anisakis* spec. 1)	Namibia Coast, Southwest Africa	Reimer (1993)
1995	Gemfish (*Rexea solandri*)	Nematoda (*Anisakis* sp. type 1), Cestoda plerocercoid (*Hepatoxylon trichiuri* and *Nybelinia* sp.)	Southern Australia	Sewell and Lester (1995)
1995	Hake (*M. australis* and *M. hubbsi*)	Cestoda plerocercoid (*Grillotia* sp. and *Hepatoxylon trichiuri*), Copepoda (*Trifur tortuosus*) and Digenea (*Elytrophalloides oatesi*)	Southern Chile, Falkland Islands and Argentine shelf	MacKenzie and Longshaw (1995)
1995	Sailfish (*Istiophorus platypterus*)	Cestoda (*Callitetrarhynchus gracilis* and *Otobothrium dipsacum*), Copepoda (*Pennella instructa*) and Trematoda (*Cardicola grandis*)	East Coast Australia	Speare (1995)
1997	Sablefish (*Anoplopoma fimbria*)	Trematoda (*Derogenes varicus*, *Genolinea laticauda*, and *Lecithaster gibbosus*)	Seamounts off Vancouver Island, British Columbia	Whitaker and McFarlane (1997)
1997	Atlantic Cod (*Gadus morhua*)	Copepoda (*Lemaeoceru brunchialis*), Trematoda (*Hemiurus levinseni*)	Northern Norway	Larsen et al. (1997)
2002	Chilean Hake (*M. gayi gayi*)	Larval Cestoda (*Clestobothrium crassiceps and Hepatoxylon trichiuri*), Monogenea (*Anthocotyle merlucci*) and Copepoda (*Neobrachiella insidosa f. pacifica*)	Chile and Peru	Oliva and Ballón (2002)
2003	Argentine Anchovy (*Engraulis anchoita*)	Monogenea (*Pseudanthocotyloides heterocotyle*), Digenea (Cardiocephaloides sp., *Lecithochirium microstomum*, and *Parahemiurus merus*), Larval Cestoda (*S. polymorphus*), Acanthocephala Cystacanth (*Corynosoma australe)*, Larval Nematoda (*A. simplex*, *Contracaecum* sp. & *H. aduncum)*	Southwest Atlantic, South America	Timi 2003
2003	Deepwater Redfish (*S. mentella*)	Copepoda (*S. lumpi*), Nematoda (*Anisakis simplex* and *Hysterothylacium aduncum*)	Northwest Atlantic coast, Canada	Marcogliese et al. (2003)
2004	European Hake (*M. merluccius*)	Larval Nematoda (*Anisakis* spp.)	East Atlantic Ocean and Mediterranean Sea	Mattiucci et al. (2004)
2006	Baltic Herring (*C. harengus*)	Larval Nematoda (*A. simplex*)	Baltic Sea	Podolska et al. (2006)
2007	Anchoveta (*E. ringens*)	Monogenea (*Pseudanthocotyloides heterocotyle*), Copepoda (*Caligus* sp.), Isopoda *(Livoneca* sp.), adult Cestoda *(Bothriocephalus* sp.), larval Nematoda *(Anisakis* sp. and unidentified anisakid)	Chile and Peru	Valdivia et al. (2007)

Table 1 continued

Year	Fish species	Parasite species	Study location	References
2007	Atlantic Croaker (*Micropogonias undulatus*)	Monogenea (*Diplectanotrema* sp., *Encotyllabe* sp., and *Macrovalvitrematoides micropogoni*), Digenea (*Diplomonorchirs leistomi*, *Opecoeloides fimbriatus*, and *Stephanostomum tenue*), Aspidogastrea (*Lobatostoma ringens*), Acanthocephala (*Dollfusentis chandleri* and *Serrasentis sagittifer*)	Western north Atlantic Ocean	Baker et al. (2007)
2007	Atlantic Horse Mackerel (*Trachurus trachurus*)	Trematoda (*Derogenes varicus*, *Ectenurus lepidus*, and *Tergestia latticolis*), Monogenea (*Gastrocotyle trachuri*, *Heteraxinoides atlanticus*, *Pseudaxine trachuris*	Northeast Atlantic	Campbell et al. (2007)
Unpublished	Pacific Sardines (*Sardinops sagax*)	Trematoda (*Parahemiurus* sp.)	Ecuador and Peru	MacKenzie et al. (unpublished)

pattern limited to the PNW was identified by the distribution of the trematode *Lecithaster gibbosus* (Baldwin 2010 Ph.D. dissertation), a generalist parasite infecting 82 fish species across the North Pacific Ocean from Oregon to Japan (Pratt and McCauley 1961; Love and Moser 1983; McDonald and Margolis 1995; Moles 2007). Out of 1,389 sardines examined, only seven were infected with both *L. gibbosus* and *M. ecaude* (six off Vancouver Island, British Columbia, and one off of Willapa Bay, Washington). Further our recovery of only three sardines off northern California infected with *L. gibbosus* suggests few sardines that overwinter off Vancouver Island, British Columbia return the following spring to spawn off Southern California (Baldwin 2010 Ph.D. dissertation). If a second migration pattern exists off the PNW, then a smaller stock originating from the northern California Current may be intermingled with the migrants from southern California. Additional information on the migration behavior of Pacific sardine would benefit future studies on stock identification, especially if there is the potential for the re-establishment of the far northern stock previously described by Radovich (1962, 1982).

Parasite identification and discrimination: morphological and molecular characteristics

Before molecular techniques were available to identify parasites genetically, the ease of correctly identifying parasites taxonomically was an important consideration when choosing parasites as biological tags. The ability to distinguish between parasite species has traditionally relied upon taxonomic keys based upon the morphology of adult worms. These keys compare the variation in characteristics that define a particular family, genus, or species, but are difficult to use for identifying larval stages of parasites. However, with the development of molecular markers for parasites, it is now possible to identify all developmental stages to species even of parasites with complex life-cycles (Criscione et al. 2005, Locke et al. 2010). Individual parasite species can be morphologically similar but genetically different (Criscione et al. 2005; Mattiucci 2006). Cryptic species arise when genetic variation between closely related species is less conserved than morphological characteristics (Jousson et al. 2000). With

the increasing availability of parasite DNA sequences, cryptic species have been discovered among several parasite taxa (Criscione and Blouin 2004; Vilas et al. 2005), and have altered our understanding of the geographic ranges of some platyhelminthes (Jousson et al. 2000). Mattiucci et al. (2004) used allozyme differences to demonstrate that seven genetically distinct species existed among morphologically similar individuals of *Anisakis* species collected from European hake (*Merluccius merluccius*). *Anisakis simplex*, originally considered a cosmopolitan species found globally, is now recognized as a mixture of nine genetically distinct species distributed across a large geographical area (Mattiucci et al. 2009). Vilas et al. (2005) suggested that parasite populations should be examined for cryptic species when parasite individuals are found in several habitats or host species.

The relative mutation rates of homologous loci between parasite DNA and that of their hosts suggests that some parasites have a faster generation time than hosts (Whiteman and Parker 2005), thus accumulating genetic variation faster and enabling host population structure to be inferred from parasite population structure. For example, Hafner et al. (1994) concluded that the mutation rates of chewing lice (*Geomydoecus* spp. and *Thomomydoecus* spp.) were approximately three times faster than those of their pocket gopher hosts (*Orthogeomys* spp., *Zygogeomys* sp., *Pappogeomys* sp., *Cratogeomys* sp., *Geomys* sp., and *Thomomy* sp.). This implies that divergence times separating parasite populations would be shorter than those separating host populations. Criscione et al. (2006) indicated that parasite genotypes of the trematode *Plagioporus shawi* were more accurate in assigning an individual steelhead trout (*O. mykiss*) to its natal stream than genotypic data of the fish. F_{st} values were ten times greater for *P. shawi* than for steelhead, suggesting less gene flow between parasite populations than steelhead populations. Additional findings by Marcogliese et al. (2003) and Criscione and Blouin (2006) indicated that parasite genotypes supported fish management boundaries defined by other methods.

Similar to fish genetic data, results using parasite genetic data may differ depending on the type of molecular marker used, and may thus lead to different interpretations of stock identity. For example, Vilas et al. (2005) compared mitochondrial and ribosomal DNA sequences from the freshwater trematode *P. shawi*. They determined that mtDNA markers NADH dehydrogenase1 (ND1) and cytochrome oxidase subunit 1 (CO1) had accumulated base pair substitutions at a faster rate than that of the internal transcribe spacer ribosomal markers (ITS1 and ITS2). Cross et al. (2007) also reported high substitution rates in mtDNA CO1 sequences from *A. simplex s.s.* infecting Atlantic herring (*C. harengus*). If the molecular marker chosen has a slow mutation rate, then parasite subpopulations that have recently been separated may still be noted as undifferentiated and mistakenly considered one population.

Gene flow between parasite populations is influenced by the mobility of host species (Prugnolle et al. 2005; Criscione et al. 2006). For instance, Criscione and Blouin (2004) suggested that parasites with allogenic life cycles (definitive host a mammal or bird) had more gene flow between distant populations than parasites with autogenic life cycles (definitive host a fish). This was expected, since geographic barriers are less likely to influence the movement of birds or mammals than fish. Thus more than one type of molecular marker and parasite should be examined from a given host under study to improve the understanding of parasite genetic structure and to determine which parasites are best suited as biological tags.

Recommendations on parasite molecular markers

In addition to the ecological characteristics important to identify candidate parasite biological tags, the characteristics and approaches necessary for parasite molecular markers include: (1) ease of recovery and identification (Aiken et al. 2007); (2) use of more than one genetic marker to verify that a parasite species is cryptic (Vilas et al. 2005); (3) an assessment of mutation rates when choosing a specific genetic marker type (Vilas et al. 2005); (4) temporal and geographic stability in a parasite population to enable long-term monitoring of parasite populations (Cross et al. 2007); and (5) use of parasite phylogeography to infer host population structure (Mattiucci and Nascetti 2008).

Integrating techniques for fish stock identification

The techniques chosen to identify subpopulations or stocks, and the boundaries separating these stocks,

are critical for understanding and managing fish species. For instance, if small and locally important stocks of Pacific sardine exist off California and the Pacific Northwest, their identity could be masked by managing fish over this large geographical scale as one fishery. Recently the HOMSIR (Horse Mackerel Stock Identification Research) project assessed the stock structure of horse mackerel (*Trachurus trachurus*) in the northeast Atlantic and Mediterranean Sea in 2000 and 2001 (Abaunza et al. 2008a). A combination of fish genetics, morphometrics (e.g., body shape), life history traits (e.g., distribution) and parasite community and genetics data (Abaunza et al. 2008a, b; MacKenzie et al. 2008; Mattiucci et al. 2008) were examined from the same individual fish. The parasite community and fish morphometrics provided the strongest evidence for the presence of separate stocks within the Atlantic Ocean (western and southern) and the North Sea. Parasite allozyme data further separated fish from the Mediterranean Sea into three different stocks, and provided evidence that horse mackerel may move between the southern Atlantic and the western Mediterranean (Abaunza et al. 2008b; Mattiucci et al. 2008). Thus, the successful integration of multiple techniques in a holistic approach (Begg and Waldman 1999) can enable the discovery of distinct fish stocks.

Requirements for a Pacific sardine study

The sampling design of the HOMSIR project can be adapted to conduct a stock identification project for Pacific sardine in the California Current. Previous information from both scientific surveys and fishing effort is available on the distribution, abundance, demographic structure, growth and reproduction of Pacific sardines (e.g. Smith 2005; Checkley et al. 2009). Regional studies on Pacific sardine have been done previously throughout the California Current, but not necessarily during the same years (Emmett et al. 2005; McFarlane et al. 2005; Smith 2005, Lo et al. 2010). A variety of genetic methods (to determine evolutionary history) and phenotype marker techniques (to study short-term changes due to the environmental variation) would be included such as gill raker counts, fish age using otoliths, otolith shape and microchemistry, and genetics of both sardines and parasite taxa. Also the ecosystem structure required for Pacific sardines throughout the California Current could be compared by analyzing sardine diet, parasite species composition and abundance, and physical environmental data (such as sea surface temperature, salinity, and chlorophyll-a).

The relative abundance of Pacific sardine is not static in the California Current during the year (Lo et al. 2010). For example, it is unclear if a lack of Pacific sardine migrating from southern California or a decline in successful spawning is leading to a reduced abundance off the PNW since 2003 (Lo et al. 2010). Ideally, a sampling program would encompass the known distribution of the Central California offshore stock from Vancouver, British Columbia to Ensenada, Baja California (Smith 2005, Lo et al. 2010). As suggested by Lo et al. (2010) a coastwide survey conducted during the spring and summer of the same year would enable the spawning area in the PNW to be defined, and compared with the spawning biomass already examined during April of each year for a stock biomass estimate (e.g. Hill et al. 2010). The contribution of egg production in the PNW to the overall sardine biomass, and the influence of sardine spawning in southern California to fish in the PNW should be examined (Lo et al. 2010). Additional regional surveys in the PNW during the summer and fall could reduce the uncertainty around migrants versus residents, confirm if fish ≥190 mm standard length are migrant fish (Lo et al. 2010), and clarify the existence of a second migration route identified by the distribution of the trematode *L. gibbosus* (Baldwin 2010 Ph.D. dissertation). A better understanding of the distribution of age cohorts could be clarified if samples are collected from both nearshore (on the continental shelf to the shelf break which is approximately 180 m), and offshore stations (off the continental shelf, greater than 180 m).

Oceanographic conditions vary latitudinally and longitudinally in the California Current and can influence the distribution of Pacific sardines over time and space. The distribution of Pacific sardines off Canada is limited by ocean temperature (northern range from 53 to 54°N Latitude), with fish often found in inlets off the west coast of Vancouver Island, British Columbia. The success of sardines spawning in Canadian waters has been sporadic due to the cold water temperatures in part from the equatorward movement of the Alaska Current. Sardine recruits that are present tend to stay in

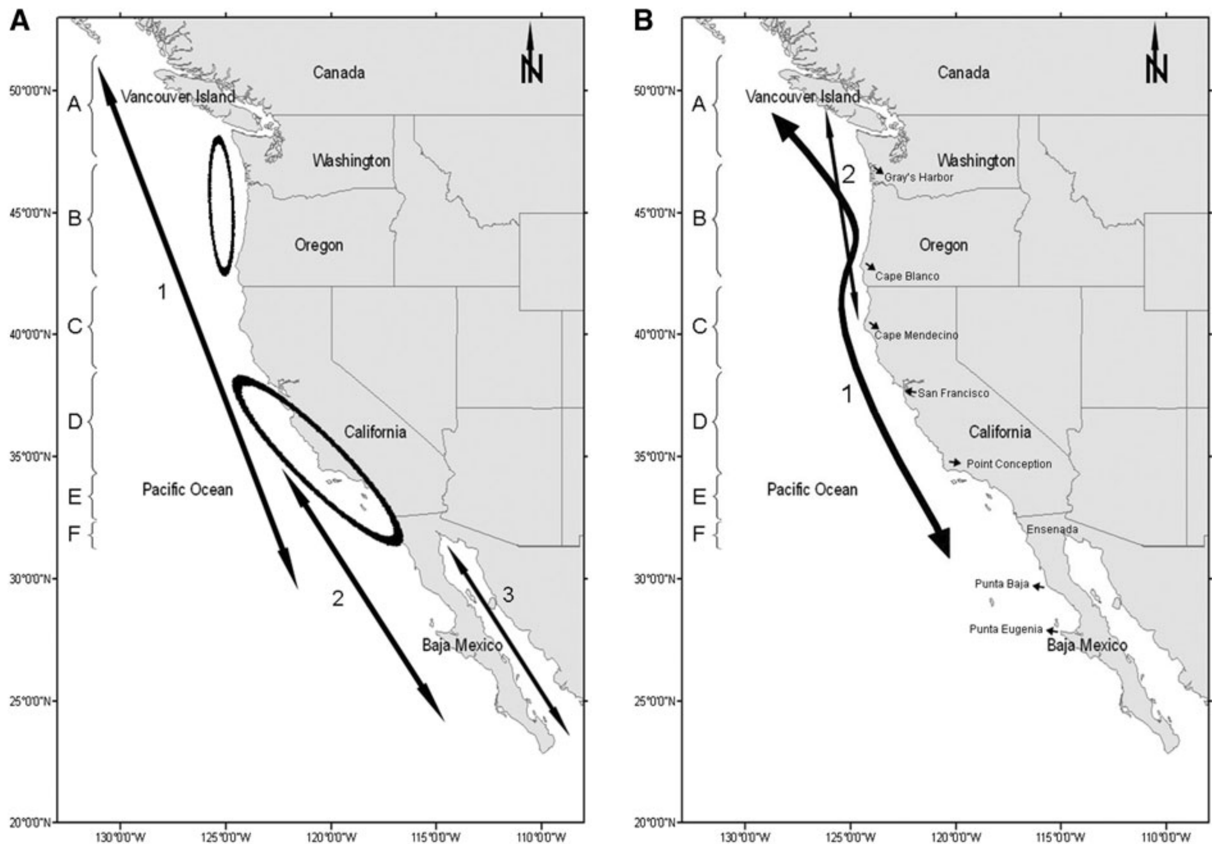

Fig. 1 Map of the California Current summarizing: (**A**) spawning locations of the Central California offshore stock (*black ovals*) of Pacific sardine (*Sardinops sagax*) based on Checkley and Barth (2009), and the distribution of the three stocks of the Pacific sardines labeled as 1 (Central California offshore), 2 (Baja Sur inshore), and 3 (Gulf of California) (based on Smith 2005) and (**B**) Two migration patterns of the Pacific sardine labeled as 1 (a coastwide pattern for individual fish >190 mm standard length), and 2 (our proposal for a second migration pattern limited to the Pacific Northwest based on the recovery of the trematode *Lecithaster gibbosus*). We also indicate a proposed sampling design for the Central California offshore stock with the California Current broken up into six sampling regions (*A* through *F*)

coastal waters, and there is evidence of juvenile and adult sardines overwintering in inlets along with schools of Pacific herring (McFarlane et al. 2005).

There is seasonal upwelling (spring through summer) and downwelling (fall through winter) off Washington and Oregon, with the potential of water jets north of Cape Blanco and eddy formation south of Cape Blanco (Checkley and Barth 2009). Suitable water temperatures for spawning are possible offshore in lower salinity water due to the stratification of the upper water column from a large input of freshwater from the Columbia River (Bakun 1996). It is unclear how a variable area of hypoxia off Heceta Bank (Grantham et al. 2004) would influence migration, spawning and successful recruitment for both migrants and residents of Pacific sardine. It is also unclear how many fish overwinter, and do not migrate back to southern California to spawn.

Southern California is considered the center for the Central California offshore stock (Lo et al. 2010). The regional area for spawning is from San Francisco to San Diego, California, however, the center of spawning can move latitudinally and longitudinally in relation to current ocean conditions. Upwelling exists all year round off California, although intensity is highest from March through September (Bakun 1996; Checkley and Barth 2009). Upwelling is weaker in the southern California Bight, and eddys produced from the upwelling zone near the Bight may increase survival of fish larvae retained in the nutrient rich water (Lynn 2003). Seasonal upwelling in the spring and summer also occur off Baja,

California with most intense upwelling at Punta Baja, located south of Ensenada, Baja, California (Lluch-Belda et al. 2003). Sampling off Baja, California also needs to consider the potential for geographic overlap of the Central California offshore stock with individuals from the Baja California Sur inshore stock (Félix-Uraga et al. 2004; Smith 2005) (Fig. 1).

During a coastwide survey, a coordinated sampling effort may best be achieved by dividing the known distribution of the Central California Offshore stock into six regions (Fig. 1): (A) Northern Vancouver Island, British Columbia to just above Grays Harbor, Washington; (B) Willapa Bay, Washington to just south of Cape Blanco, Oregon.; (C) Oregon—California State border to San Francisco, California; (D) south of San Francisco, California to just north of Point Conception, (E) Point Conception to San Diego, California; and (F) United States—Mexico country border to Ensenada, Baja, California. As suggested by Lo et al. (2010) sampling should be conducted at night to gain access to the Pacific sardine biomass in the upper 50 m of water column. For each survey, a minimum of 100 fish should be collected within each region with 50 fish caught in one haul at a nearshore station, and 50 fish caught in one haul at an offshore station. Thus, a minimum of 1,200 fish could be caught during 1 year of a coastwide survey. For some techniques more fish may be required to achieve enough power in the sampling effort. All techniques would be conducted on the same specimens to reduce the inherent variability among individual fish. To conduct a parasite community survey, each fish would need to be frozen at sea in individually labeled bags and brought back to shore for processing (Abaunza et al. 2008a). Length and weight should be measured prior to freezing. Finally, opportunistic sampling of young-of-the-year fish (<120 mm SL) within these six regions could help clarify sampling noise in the genetics and otolith microchemistry data, since these fish remain in or near the regional area they were spawned (Lo et al. 2010).

Conclusion

Fishing pressure can affect subpopulations differently, which can result in a loss of genetic diversity, and the overharvest of small subpopulations compared to larger subpopulations (Stephensen 1999). High fishing pressure along with unfavorable ocean conditions can result in a dramatic decline of species diversity and fish biomass (Beamish et al. 2004; Alder et al. 2008), and fish may be less resilient at the edges of their distribution (Beverton 1998; Powles et al. 2000). However, it remains uncertain how the synergistic effects between these factors threaten the population genetic structure of exploited fish species (Alder et al. 2008; Casini et al. 2009), and the sustainability of marine ecosystems (Harley and Rogers-Bennett 2004; Crowder et al. 2008). When it is difficult to resolve the population structure of marine fish (such as the current situation with Pacific sardine), an integrated approach that includes both fish and parasite data could clarify ecological and evolutionary events that structure fish populations. The HOMSIR project, which employed this integrated approach, should serve as an important model for future stock structure studies, especially for pelagic fish species whose populations fluctuate in response to changing environmental conditions.

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