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ORIGINAL ARTICLE

Evolutionary and biogeographical patterns within the smelt genus *Hypomesus* in the North Pacific Ocean

Katriina L. Ilves* and Eric B. Taylor

Department of Zoology, Biodiversity Research Centre, Native Fishes Research Group, University of British Columbia, 6270 University Boulevard, Vancouver, BC V6T 1Z4, Canada

ABSTRACT

Aim We address questions about trans-Pacific distributions of marine organisms and the North Pacific Ocean as a centre of marine biodiversity through a phylogenetic and biogeographical study of a pan-Pacific genus of Northern Hemisphere smelts (*Hypomesus*, Pisces: Osmeridae).

Location North Pacific Ocean.

Methods Relationships of the five species of *Hypomesus* from throughout the North Pacific were reconstructed through maximum likelihood and Bayesian phylogenetic analyses of sequence data from two mitochondrial (cyt*b*, 16S) and three nuclear (ITS2, S71, RAG1) gene regions of five to 25 individuals per species, totalling 3588 characters. The resulting phylogenies were used to test hypotheses of species relationships and geographical origins using both dispersal-based and maximum likelihood methods for inferring ancestral areas (LAGRANGE). Cyt*b* sequence divergence and a Bayesian approach (BEAST) were used to estimate the timeframe of *Hypomesus* evolution, which was compared with work on similarly distributed taxa.

Results Hypothesized trans-Pacific Ocean relationships based on lateral line scale counts were not supported by the phylogeny, suggesting parallel evolution of this phenotype, although we found one such relationship between the western *H. japonicus* and the two eastern Pacific species (*H. pretiosus* and *H. transpacificus*). Dispersalist approaches rejected an early proposal of a double-compression vicariant mechanism as well as an eastern Pacific origin. Results from the LAGRANGE analysis suggested a more widespread ancestor, although also supporting a role for the western Pacific. Divergence estimates suggested that most splits between species occurred in the mid-Miocene, and the most recent speciation event, between the eastern Pacific species, occurred in the Pliocene to early Pleistocene.

Main conclusions Our molecular data indicate that the character historically used to define relationships within *Hypomesus*, lateral line scale count, does not reflect ancestry within the genus. Biogeographical reconstructions suggest an important role for the western North Pacific in the diversification of *Hypomesus*. While uncertainty remains over the date of origin for this genus, estimates place the divergences during periods of climatic cooling that have been important in generating diversity in a number of similarly distributed organisms. Additional comparative data will provide further insight into the relative importance of the western region in generating diversity in the North Pacific Ocean.

Keywords

Biogeography, centre of origin, *Hypomesus*, marine biogeography, mitochondrial DNA, nuclear DNA, Osmeridae, parallel evolution, phylogenetic analysis, trans-Pacific distributions.

*Correspondence: Katriina Ilves, Biodiversity Research Centre, Native Fishes Research Group, University of British Columbia, 6270 University Boulevard, Vancouver, BC V6T 1Z4, Canada.
E-mail: ilves@zoology.ubc.ca

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INTRODUCTION

As an important evolutionary centre for marine diversity (Briggs, 2003), the temperate and boreal North Pacific Ocean offers an ideal setting for conducting comparative biogeographical analysis (Amano & Vermeij, 2003). In contrast to the focus on diversity 'hotspots' in the southern oceans (Briggs, 2000, 2004; Santini & Winterbottom, 2002) and biogeographical studies on North Atlantic taxa (Wares & Cunningham, 2001; Addison & Hart, 2005; Vermeij, 2005), there has been relatively little recent work exploring patterns of diversity across the entire North Pacific (although see Amano *et al.*, 1993; Collins *et al.*, 1996; Stepien *et al.*, 2000; Hyde & Vetter, 2007).

TRANS-PACIFIC DISTRIBUTIONS

A long-recognized distributional pattern in the North Pacific, however, is the existence of amphi- or trans-Pacific taxa (Andriashev, 1939; Golikov & Tzvetkova, 1972; Briggs, 1974), where a taxon is found in the eastern and western Pacific, but is absent from the northern region. This distribution has been documented in a variety of taxonomic groups, including fishes (Andriashev, 1939), crustaceans (Schweitzer, 2001), molluscs (Amano & Vermeij, 1998, 2003), polychaetes (Uschakov, 1971) and mammals (Deméré *et al.*, 2003).

Explanations for these disjunct distributions have generally postulated that changes in climate compressed the range of more widely distributed ancestors during periods of global cooling, thereby facilitating differentiation and/or allopatric speciation on opposite sides of the Pacific (Andriashev, 1939; McAllister, 1963; Briggs, 1974; Amano *et al.*, 1993). Additional hypotheses, such as changes in oxygen distribution (White, 1987), long-distance dispersal (Rosenblatt & Waples, 1986) and reinterpretations of the Earth's geological history (McCarthy, 2003, 2005) have also been suggested to explain amphi-Pacific distributions.

CENTRES OF ORIGIN

In addition to questions about the timing and possible causes of amphi-Pacific distributions, identifying the area of origin of amphi- or Pan-Pacific taxa within the North Pacific has also been of interest. For many organisms, it is assumed that the area that currently houses the highest diversity is the area of origin (Briggs, 1974), although this assumption is often not tested within a phylogenetic framework, a prerequisite to understanding a group's biogeography. Furthermore, many analyses of groups that have amphi- and/or pan-Pacific distributions have focused on different questions, and have therefore had a narrow or incomplete taxonomic and/or geographical focus, or have not explicitly linked phylogeny and geography, making it difficult to make basin-level inferences of origin from the results. Exceptions to this general lack of data are the large body of work on intertidal molluscs (Amano *et al.*, 1993; Titova, 1994; Collins *et al.*, 1996; Reid *et al.*, 1996) and recent studies on Pacific perciform fishes (Bernardi & Bucciarelli, 1999; Stepien *et al.*, 2000; Kai *et al.*, 2003; Hyde & Vetter, 2007).

STUDY SYSTEM

Here we conduct a molecular phylogenetic analysis of the Pan-Pacific smelt genus *Hypomesus* Gill (1862) (Pisces: Osmeridae) to further our understanding of evolution within this group. We also explore general questions regarding amphi- and pan-Pacific taxa and important areas of origin in the North Pacific Ocean. With six currently recognized species (Eschmeyer, 2006, http://www.calacademy.org/research/ichthyology/catalog/), *Hypomesus* is the most species-rich genus of the Northern Hemisphere smelts, Osmeridae, a family of small, silvery, lower euteleost fishes found in near-shore marine and coastal freshwaters throughout the Holarctic (McAllister, 1963). Of these six species, three are found in the western Pacific [*H. chishimaensis* Saruwatari *et al.*, 1997; *H. nipponensis* McAllister (1963) and *H. japonicus* Brevoort (1856)], two in the eastern Pacific [*H. pretiosus* Girard (1854) and *H. transpacificus* McAllister (1963)], and one [*H. olidus* Pallas (1814)] has a northern Pacific and Arctic distribution (Fig. 1).

Hypomesus has a complicated taxonomic history. Original subspecies classifications *H. pretiosus pretiosus*, *H. p. japonicus*, *H. transpacificus transpacificus* and *H. t. nipponensis*, with *H. olidus* at full species rank, imply sister relationships between species on opposite sides of the North Pacific Ocean (McAllister, 1963). If these classifications reflect ancestry, they require at least two replicate divergences across the ocean basin. Subsequent revisions led to the elevation of all taxa to full species status (Klyukanov, 1970; Saruwatari *et al.*, 1997). Saruwatari *et al.* (1997) also reinforced the pre-eminence of lateral line scale counts in ascertaining relationships, as suggested by McAllister (1963), by introducing the idea of species groups based on these counts. A 'high' scale-count group contained *H. japonicus* and *H. pretiosus*; *H. nipponensis* and *H. transpacificus* were classified in a 'low' scale-count group; and *H. olidus* was placed in its own group. These relationships reflected the original subspecies designations. Saruwatari *et al.* (1997) also identified a new species from the freshwaters of the Kuril Islands, *H. chishimaensis*, which was placed in the 'nipponensis' grouping. Recent morphological (Sidorov & Pichugin, 2004) and genetic (Ilves & Taylor, 2007) work failed to detect any differences between the populations assigned to this new species and those assigned to *H. nipponensis*; therefore in this study we consider *H. chishimaensis* to be a synonym of *H. nipponensis*.

JUSTIFICATION OF METHODS

Inferring ancestral states is a rapidly developing field in phylogenetic analysis, with parsimony (Maddison & Maddison, 2003, 2006), maximum likelihood (ML, Schluter *et al.*, 1997; Ree *et al.*, 2005; Maddison & Maddison, 2006) and Bayesian (Bollback, 2006) methods available. Methods in

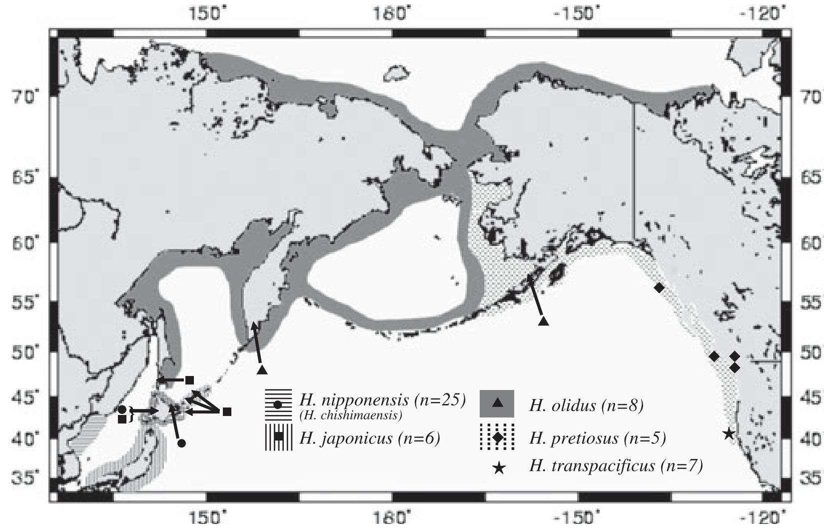

Figure 1 Approximate distribution map of the five species of *Hypomesus* in the North Pacific Ocean with sample numbers and locations. Distribution information from McAllister (1963), Saruwatari *et al.* (1997) and FishBase (Froese & Pauly, 2006).

which geographical area is mapped onto a phylogeny and optimized on nodes are frequently used (Smith *et al.*, 2005; Baker *et al.*, 2006; Jones *et al.*, 2006), but have also been criticized for a number of reasons, particularly because distributional area is not inherited in the same manner as Mendelian characters (Ree *et al.*, 2005). Further, such methods, which assume a dispersalist or centre-of-origin mechanism, have been much criticized in the vicariance biogeography literature (Croizat *et al.*, 1974; Nelson & Platnick, 1981; Ebach, 1999; Humphries & Parenti, 1999).

The decision as to whether to follow a strict dispersalist or a vicariance biogeography approach for a particular study can be made in several ways, individually or in combination.

1. An ideological attachment to one idea over the other would lead to the choice and exclusion of particular methods.

2. There may be *a priori* information that makes one scenario more biologically and/or geologically more likely for the group in question [e.g. known timing of divergences correlates to fragmentation of continents (vicariance); volcanic origin of islands (dispersal)].

3. *A posteriori* information may suggest that one mechanism was more important for generating the distributions of the group in question [e.g. a phylogeny shows one area occupied only by most recently diverged species (dispersal)].

Early hypotheses of Osmeridae evolution (McAllister, 1963) developed from a centre of origin perspective, and we therefore think it is appropriate to test those hypotheses from that framework [cf. point (1) above]. Furthermore, we agree with McDowall (2002), de Queiroz (2005), Cowie & Holland (2006) and others that, in addition to vicariance, dispersal is and has been an important mechanism in generating distributions, and that a widespread ancestor is unlikely in many cases, such as when a taxon is composed of geographically restricted taxa (Bremer, 1992). As this is the situation with *Hypomesus*, we do not feel that a widespread ancestor for this genus should necessarily be the null hypothesis [cf. point (2) above]. Finally, cladistic biogeographical approaches, which aim to discern bifurcating relationships between areas from taxon cladograms through a number of methods (Nelson & Platnick, 1981; Zandee & Roos, 1987; Page, 1988; Nelson & Ladiges, 1991, 1996; Humphries & Parenti, 1999 and references therein), do not capture the complexity of areas that undergo repeated and/or differential fragmentation through time (Donoghue & Moore, 2003). We do not, however, start from the assumption that vicariance was unimportant in the history of *Hypomesus*, so we also attempt to model the biogeographical history of the genus in a maximum likelihood framework, correlate the timing of divergences within the genus to known cooling events in the Cenozoic history of the North Pacific Ocean, and compare these divergence times with those of other, similarly distributed organisms.

To address the question of area of origin, we use two basic approaches: a dispersalist, centre-of-origin approach, and a newly developed ML modelling method that incorporates both dispersal and vicariance (Ree *et al.*, 2005). The first parsimony-based approach, implemented in MESQUITE ver. 1.12 (Maddison & Maddison, 2006), yielded several hypotheses with testable predictions (hypotheses A–D; Fig. 2).

Hypothesis A: the proposal by McAllister (1963), subsequently supported by Saruwatari *et al.* (1997), requires two replicate divergences across the North Pacific to generate the scale-count relationships between putative amphi-Pacific sister species. In a parsimony framework, the expected phylogeny (provided this phenotype reflects ancestry) shows sister relationships between species with similar scale counts (Fig. 2a).

Hypothesis B: what we consider an *a priori* most parsimonious explanation (Fig. 2b), consistent with the idea of range compression due to climate cooling, begins with a northern ancestor followed by a single split across the North Pacific and differentiation on each side.

Hypothesis C: eastern Pacific origin of *Hypomesus*, followed by dispersal to northern and western areas (Fig. 2c).

Hypothesis D: western Pacific origin of *Hypomesus*, followed by dispersal to northern and eastern areas (Fig. 2d).

The ML approach in LAGRANGE, on the other hand, incorporates phylogenetic and palaeogeographical information about

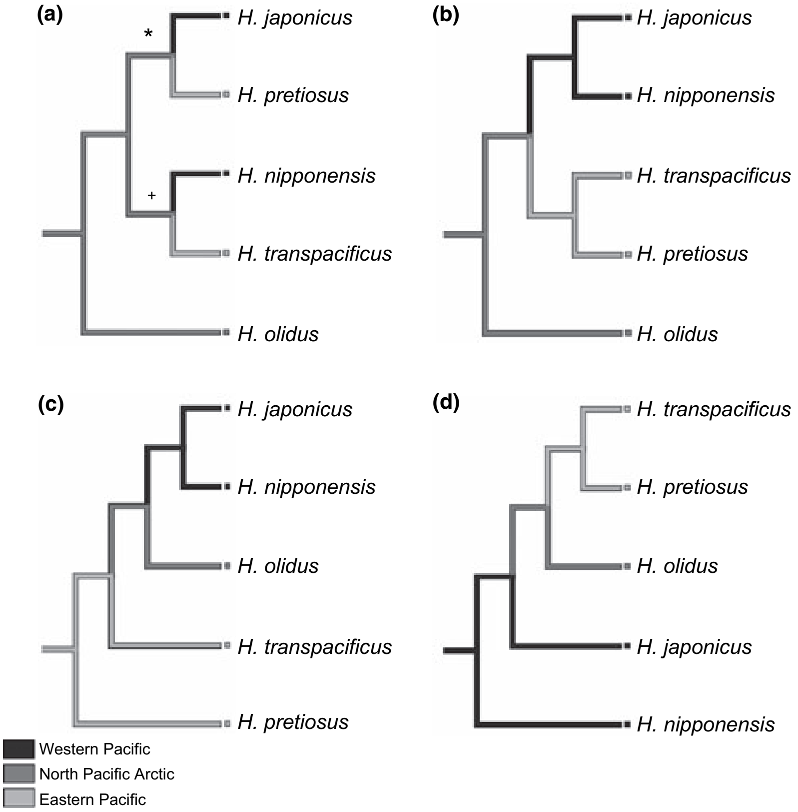

Figure 2 Parsimony-based expected phylogenies of *Hypomesus* with the geographical ranges of the species. (a) Three species groups with two replicate divergences across the North Pacific required McAllister (1963). * and + represent high and low scale-count groups, respectively. (b) *A priori* hypothesis with single split across the North Pacific (c) eastern Pacific; (d) western Pacific origin. *Hypomesus olidus* is assigned a northern Pacific distribution. Characters are ordered such that two steps are required between the west and east Pacific. Interchanging the terminal taxa from the same geographical range in (b–d) would result in the same interpretation. See text for further discussion.

the timing and extent of connections between different areas, and calculates fractional likelihoods for different biogeographical scenarios at each node of the phylogenetic tree (Ree *et al.*, 2005). This approach may yield both dispersalist and vicariance interpretations, which can then be compared with patterns seen in other, similarly distributed taxa.

AIMS

From a phylogenetic analysis of five gene regions (two mitochondrial, three nuclear) with multiple individuals per species, we aim to: (1) clarify the evolutionary relationships within a genus of systematically problematic fishes, (2) determine whether the subspecies designations based on scale counts reflect ancestry, or instead whether the shared phenotype is a result of parallel evolution, (3) use several methods to test different biogeographical hypotheses of *Hypomesus* evolution to determine the likely area of origin of this genus, and (4) put these results in a comparative framework to contribute towards an understanding of biogeographical relationships in the North Pacific.

MATERIALS AND METHODS

Taxon sampling

Samples used (Table 1) represent the five *Hypomesus* species and the outgroup *Mallotus villosus* Müller (1776) [a species within the Osmeridae, outside *Hypomesus* (K.L.I., unpublished data) based on phylogenetic analysis of five gene regions].

Table 1 Number of sequences for the five gene regions for *Hypomesus* species and the outgroup *Mallotus villosus*. The range number of base pairs for each gene (excluding indels) is indicated in parentheses.

	Gene region (bp)				
Species	Cyt*b* (285–425)	16S (495–547)	ITS2 (247–441)	S71 (338–732)	RAG1 (742–1440)
H. japonicus	6	6	6	6	5
H. nipponensis (*H. chishimaensis*)	20	25	25	24	14
H. olidus	8	5	4	8	3
H. pretiosus	5	5	5	5	2
H. transpacificus	7	7	7	7	5
M. villosus	2	2	2	2	2

Samples for '*H. chishimaensis*' were obtained from the two southernmost main chain Kuril Islands (Kunashir and Iturup), one of the Habomai group islands (Zeliyoni) of Japan, and Sakhalin Island, Russia. *Hypomesus nipponensis* and *H. japonicus* samples came from two locations on Hokkaido, Japan; *H. olidus* samples originated from Kamchatka, Russia and Chignik, Alaska (Fig. 1). The two eastern Pacific species were represented by *H. pretiosus* from Sumner Strait, Alaska, USA; two locations in British Columbia, Canada (Wreck Beach, Vancouver, and Bamfield, west coast of Vancouver Island); and the San Juan Islands, WA, USA, and by *H. transpacificus* from the Sacramento River, CA, USA. The two *M. villosus* outgroup individuals were from locations in British Columbia, Canada: the central coast and Trevor Channel on the west coast of Vancouver Island.

Voucher specimen and locality information are provided in Appendix S1 in Supplementary Material. GenBank accession numbers for all sequences used in this study are provided in Appendix S2. Phylogenetic trees from analysis of the mitochondrial, nuclear, and all data combined have been submitted to TreeBase [S1807 (study), M3307-M3309 (mtDNA, nDNA, allDNA, respectively)].

DNA sequence data

Sequence data for two mitochondrial and three nuclear gene regions were obtained for multiple individuals of the five species within the genus (Table 1). These regions included mitochondrial (mtDNA) protein-coding cytochrome *b* (cyt*b*; Kocher *et al.*, 1989) and large ribosomal subunit (16S; Waters *et al.*, 2002) and nuclear (nDNA) internal transcribed spacer (ITS2; Presa *et al.*, 2002), first intron of the ribosomal S7 protein (S71; Chow & Hazama, 1998) and the protein-coding recombination activating gene (RAG1; Quenouille *et al.*, 2004). Use of these markers in a previous study on *Hypomesus* showed them to have varying degrees of divergence, making their combined use fruitful for phylogenetic studies (Ilves & Taylor, 2007). DNA extraction, PCR and sequencing protocols were performed as described by Ilves & Taylor (2007).

Phylogenetic analyses

Sequences were aligned using ClustalX (Thompson *et al.*, 1997) or manually with MacClade ver. 4.06 (Maddison & Maddison, 2003) and edited with se-al ver. 2.0a11 (http://tree.bio.ed.ac.uk/software/seal) or MacClade ver. 4.06 (Maddison & Maddison, 2003). The alignments for cyt*b*, 16S and RAG1 were unambiguous. For extra confidence in the 16S rRNA alignment, a secondary structure model presented by Waters *et al.* (2002) was followed, which showed that the few indels occurred within loop regions. Indels in the ITS2 and S71 alignments made positional homology uncertain in several locations; therefore 104 and 13 characters, respectively, were excluded from the two alignments. paup* ver. 4.0b10 (Swofford, 2002) was used to calculate pairwise distances, perform ML, parsimony, and neighbour-joining (NJ) analyses, and conduct Shimodaira–Hasegawa (SH) tests for comparing tree topologies. MrBayes ver. 3.1.1 (Huelsenbeck & Ronquist, 2001) was used for Bayesian estimates of phylogeny.

Phylogenetic analyses were conducted by individual locus as well as by combined mitochondrial, combined nuclear, and all data combined. modeltest ver. 3.6 (Posada & Crandall, 1998) was run for all data partitions (individual and combined) to select a model of sequence evolution. The model chosen by the Akaike information criterion (AIC) method of model testing was implemented for the analyses (Posada & Buckley, 2004), which corresponded to TVM + I (mtDNA), GTR + Γ (nDNA) and GTR + I (all data).

Due to the large amount of sequence data (Table 1), NJ and Bayesian analyses were run for all sequences for all the data partitions, to identify individuals of each species that represent a large range of the intraspecific variation to be included for more rigorous ML and Bayesian analyses. This first step of analysis included 1000 NJ bootstrap replicates of all sequences for each marker separately, and Bayesian analyses of all sequences for all markers combined (5×10^5 generations, burn-in 500, 4500 sampled trees). Apart from unresolved relationships within *H. transpacificus* for the 16S region and *H. pretiosus* for the ITS2 region, all species were monophyletic for each data partition. To represent intraspecific variation, therefore, the three most divergent individuals within each species clade for cyt*b*, 16S, ITS2 and S71 were chosen for inclusion in more thorough analyses (see Results). Only two *H. olidus* individuals were included as there was very little intraspecific variation for these gene regions. RAG1 sequences were not available for all individuals, so to avoid a situation of missing data, in several cases a sequence from a conspecific was substituted. Similarly, for the final analyses of ITS2, a single substitution was made for *H. olidus*. These substitutions are indicated in Appendix S2.

Bayesian analysis was conducted on all sequences for each gene region separately, for the combined data sets with all individuals, and for the combined data sets with a reduced number of individuals (see below) using the general model chosen by the AIC method in modeltest, allowing MrBayes to calculate the exact parameter values. Two parallel analyses were run for 10^6 (single locus) or 2×10^6 (combined data sets) generations with four MCMC chains, a sample frequency of 100 and a burn-in of 3000. As the stationarity of likelihoods was always observed by 2000 generations, the sampled trees were found well after stabilization.

For ML analyses on the combined data sets, heuristic searches were conducted with six random replicates of stepwise taxon addition. Confidence in groupings was assessed using 1000 bootstrap pseudoreplicates, retaining groupings that appeared with a frequency of at least 50%. To confirm concordance with the Bayesian analyses, ML analyses by locus were also conducted (100 bootstrap pseudoreplicates).

Parsimony analyses were also conducted on all reduced data sets by gene region (branch and bound searches) and combined data sets (heuristic searches, simple stepwise addition), and were assessed by 1000 bootstrap pseudoreplicates.

Finally, to assess whether or not the species groups based on lateral line scale counts reflect ancestry within *Hypomesus*, the high and low scale-count groups were mapped onto the resulting phylogenies.

Evaluating biogeographical scenarios

We used two basic approaches to evaluate biogeographical hypotheses statistically for the evolution of *Hypomesus*: dispersalist, which optimizes areas onto nodes like a character (Maddison & Maddison, 2003, 2006) and an ML method for inferring ancestral areas (Ree *et al.*, 2005). The first approach involved parsimony reconstruction of ancestral areas. First, using the SH test (Shimodaira & Hasegawa, 1999) implemented in PAUP* ver. 4.0b10 (Swofford, 2002), we compared the expected topologies under several biogeographical scenarios (Fig. 2) with topologies generated from the molecular analyses. This test compares the likelihoods of different tree topologies for a particular data set, and can assess whether one topology is significantly better than another (Felsenstein, 2004). The parsimony reconstruction method in MESQUITE ver. 1.12 (Maddison & Maddison, 2006) was also used to infer the area of origin for *Hypomesus* with *H. olidus* both restricted to the northern Pacific and polymorphic for the three areas.

For the second basic approach to evaluate different biogeographical scenarios, we implemented the ML method in the LAGRANGE program described by Ree *et al.* (2005). This method improves on the character-mapping approaches described above, in several ways. Most significantly, LAGRANGE allows different modes of inheritance so that daughter species do not necessarily inherit identical geographical ranges; multiple character states are permitted; and palaeogeographical information about when dispersal between areas was possible is integrated into the analysis (Ree *et al.*, 2005). To conduct this analysis, the following parameters are required: an ultrametric phylogenetic tree (tree that assumes a molecular clock where all tips are contemporaneous) with branch lengths, a set of areas assigned to each taxon, divergence time of root node, times and probabilities when dispersal between areas was possible, and probabilities of lineage dispersal (from) and extinction (within) areas (Ree *et al.*, 2005). By integrating all this information, LAGRANGE calculates fractional likelihoods of ancestral areas for each node of the tree.

Our implementation of this analysis was as follows. We chose a single individual to represent each species (Appendix S2) and, based on all the sequence data combined, produced an ultrametric tree using the Bayesian analysis program BEAST ver. 1.4.1 (Drummond & Rambaut, 2006; http://beast.bio.ed.ac.uk) under a log-normal relaxed molecular clock (Drummond *et al.*, 2006) and a Yule pure birth model of speciation. The results of three runs of 5×10^7 generations were compiled. Resulting divergence times for each node were calibrated based on a divergence time of 15 Ma (the origin of the Sea of Japan; Itoh *et al.*, 1997) for *H. japonicus* and the two eastern Pacific species, under the assumption that the ancestor of *H. japonicus* evolved in this basin (Table 2; see Discussion). *Hypomesus japonicus* and *H. nipponensis* were assigned a western Pacific distribution and *H. pretiosus* and *H. transpacificus* an eastern Pacific distribution. Simulations were run with *H. olidus* restricted to the North Pacific and Arctic and as polymorphic for all regions of the Pacific and Arctic. The outgroup *M. villosus* was excluded from this analysis because it is not the sister group to *Hypomesus*. The dispersal connections between areas were parameterized based on documented land-bridge connections and cooling events of the Cenozoic (Fig. 3). Connections between areas have associated probabilities of dispersal success through time, which is different from the probability of dispersal from one area to another, as discussed below. A connection between the Arctic and North Pacific oceans was allowed with a probability of 1.0 between 7 and 2 Ma, as there was no Bering land bridge during this period prior to the onset of the Pleistocene glacial cycles (Marincovich & Gladenkov, 1999). Dispersal between the northern Pacific and the western and eastern Pacific was deemed possible during

Table 2 Corrected (TIM + Γ model) cyt*b* divergences with time frame and associated climatic events (Kennett, 1982; Tsuchi, 1997; Zachos *et al.*, 2001) corresponding to *Hypomesus* divergences based on two rates of cyt*b* evolution: 1.77% (calibrated based on *H. japonicus*–*H. pretiosus*/*H. transpacificus* split (see text), and 1.56% per Myr (Stepien *et al.*, 2000), and Bayesian estimation under a log-normal relaxed molecular clock model, based on all sequence data combined, implemented in BEAST ver. 1.4.1(Drummond & Rambaut, 2006) (numbers in brackets indicate 95% CI for BEAST estimations).

Node	Corrected mean cyt*b* sequence divergence (%)	Cyt*b* divergence estimate (Ma)	BEAST divergence estimate (Ma)	Geological time period	Climatic events
1	23.6 (*H. olidus*–*H. japonicus*)	13.3–15.1	22.9 (14.5–34.4)	Early–mid-Miocene	Mid-Miocene climatic optimum
2	22.2 (*H. nipponensis*–*H. olidus*)	12.5–14.2	16.1 (9.3–23.9)	Mid-Miocene	Mid-Miocene climatic optimum followed by cooling with onset of Antarctic glaciation and formation of Sea of Japan
3	26.5 (*H. japonicus*–*H. pretiosus*/*H. transpacificus*)	15.0–17.0	15 (8.9–22.3)		
4	2.8 (*H. pretiosus*–*H. transpacificus*)	1.6–1.8	3.9 (1.1–8.2)	Mid-Pliocene–early Pliocene	Early Pliocene warm period followed by beginning of Pleistocene glacial cycles

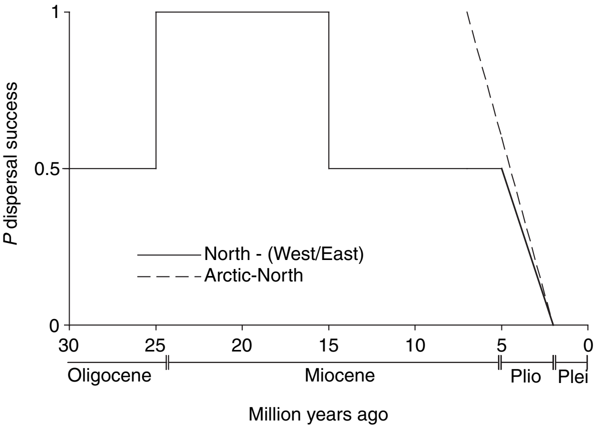

Figure 3 Probability of dispersal success (connection) between the four areas defined for the LAGRANGE analysis of ancestral area: Arctic Ocean, north Pacific, west Pacific and east Pacific oceans. The corresponding probability of dispersal success between Arctic–north Pacific and north Pacific–(west/east) Pacific through the mid-late Cenozoic is plotted. The west–east Pacific connection is described in the text. Increases and decreases in probability of dispersal success between regions correspond to periods of global warming and cooling, respectively, based on Zachos *et al.* (2001).

relatively warm periods based on Zachos *et al.* (2001): the probability of dispersal success was 1.0 between 25 and 15 Ma, corresponding to the Miocene climatic optimum, and then decreased to 0.5 at 15 Ma, where it remained until 5 Ma, with a final linear decrease to 0 between 5 and 2 Ma (Pliocene cooling to the beginning of the Pleistocene glacial period). Allowing connections during the early Pliocene warm period (5–3 Ma; Ravelo *et al.*, 2004) with a linear decrease to zero between 3 and 2 Ma did not change the results (data not shown). Two scenarios of dispersal between the western and eastern North Pacific were tested, one allowing minimal dispersal and one assuming that all dispersal between the east and west had to go through the north Pacific, roughly along the arc formed by the Aleutian and Kuril island chain, a scenario we believe more plausible for near-shore anadromous fishes. When dispersal across the Pacific was permitted, the periods corresponded to the same warm periods as described for northern–(western/eastern) connections, although with half the probability, and with a decreasing probability from 0.5 to 0 between 15 and 5 Ma (Fig. 3). Following Ree *et al.* (2005), several combinations of dispersal (λ_D) and extinction (λ_E) probabilities were run ($\lambda_D = 0.09$, $\lambda_E = 0.01$; $\lambda_D = 0.009$, $\lambda_E = 0.001$; $\lambda_D = 0.05$, $\lambda_E = 0.05$; $\lambda_D = 0.005$, $\lambda_E = 0.005$; $\lambda_D = 0.01$, $\lambda_E = 0.09$; $\lambda_D = 0.001$, $\lambda_E = 0.009$). For each λ_D, λ_E combination we ran 10^5 iterations. This was repeated five times, and for each combination the result with the highest likelihood was compiled for interpretation.

Comparisons with other North Pacific taxa

As a supplement to broad comparisons with published literature on pan- and trans-Pacific taxa, for a more direct approach we identified two groups of fishes, the surfperches (Embiotocidae) and thornyhead rockfishes (*Sebastolobus*), with amphi-Pacific relationships for which cyt*b* sequence data were available. Based on cyt*b* and 16S sequences, in the Embiotocidae, one clade within the family showed a sister relationship between two Japanese genera (the monotypic *Ditrema* and *Neoditrema*) and a clade of genera from the eastern Pacific (with the monotypic *Hypsurus* as most basal; Bernardi & Bucciarelli, 1999). In *Sebastolobus*, Stepien *et al.* (2000) found the western Pacific *S. macrochir* to be basal to the two eastern Pacific species (*S. alascanus* and *S. altivelis*) using mtDNA control region sequence divergence. Cyt*b* sequences were available for all three surfperch species (GenBank accession numbers AF159340, AF159341, AF159335; Bernardi & Bucciarelli, 1999), and two *Sebastolobus* species, *S. macrochir* (GenBank accession number AB096136; Y. Kai and co-workers, unpublished data) and *S. alascanus* (GenBank accession number AF031497; Rocha-Olivares *et al.*, 1999). To compare cyt*b* sequence divergence among amphi-Pacific taxa in these two groups with that of *Hypomesus*, uncorrected pairwise differences were calculated in PAUP* ver. 4.0b10 (Swofford, 2002).

RESULTS

Sequences

The three individuals chosen per species for the final phylogenetic analyses were representative of the intra-specific diversity for each gene region in all cases, including *H. transpacificus* and *H. pretiosus* where initial analyses were unable to determine the relationships between individuals of these species for 16S and ITS2, respectively (see Methods). These final analyses included 15 sequences (14 for RAG1) ranging from 286–425 bp (cyt*b*), 531–548 bp (16S), 287–441 bp (ITS2), 432–706 bp (S71) and 916–1431 bp (RAG1). Including indels, the combined mtDNA, nDNA and all data partitions included for analysis (117 characters excluded from the nDNA and all data partitions due to questionable alignment) contained 973, 2615 and 3588 characters, respectively.

Hypomesus phylogeny

The combined mtDNA and nDNA topologies produced through ML and Bayesian analyses (Fig. 4) initially appeared to differ in the placement of *H. japonicus*. The mtDNA tree indicated a close relationship between *H. japonicus* and the *H. nipponensis–H. olidus* grouping, whereas the nDNA data resulted in a sister relationship between *H. japonicus* and the two eastern Pacific species (Fig. 4). To determine whether or not these differences represented a true conflict between the mitochondrial and nuclear data, SH tests were performed in each data set, comparing the topology generated separately under nDNA and mtDNA data with a constraint tree that had the alternative topology (a tree constrained to the nDNA-based topology was tested with the mtDNA data, and *vice versa*).

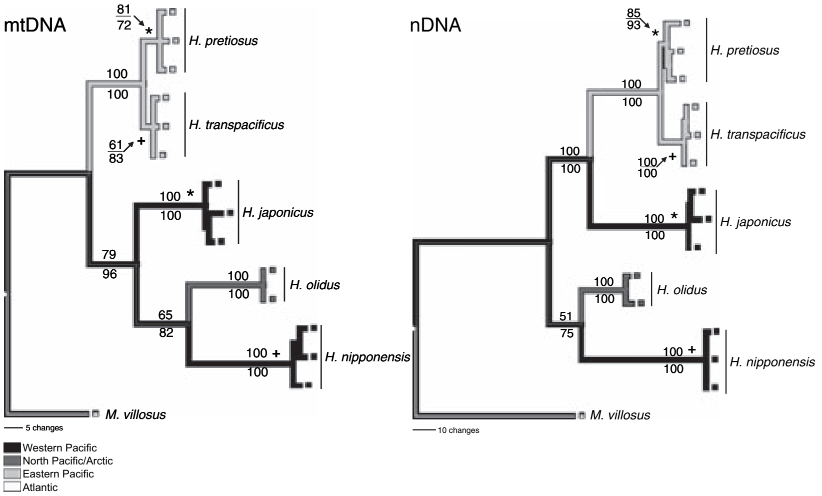

Figure 4 Combined mitochondrial (mtDNA) [cyt*b* and 16S] and nuclear (nDNA) [ITS2, S71 and RAG1] phylogenies of *Hypomesus*. *, +, Species with high and low lateral line scale counts, respectively; WPac, NPac, EPac, geographical distributions in the western, northern and eastern Pacific, respectively. Numbers above nodes represent bootstrap support values from 1000 pseudoreplicates in a maximum likelihood analysis; those below nodes are posterior probabilities from a consensus of 17,000 post-burn-in trees generated through Bayesian analysis (2×10^6 generations). *Mallotus villosus* is the outgroup. Geographical areas are mapped onto the phylogenies following the model described in Fig. 2.

With the mtDNA data set, there was no significant difference between the nDNA-based constraint tree and that generated with the mtDNA data (–2355.5 vs. –2358.1, $P = 0.21$); however, with the nuclear data set the nDNA tree was significantly better than the tree constrained to the mtDNA-based topology (–5669.5 vs. –5685.9, $P < 0.02$). The likelihoods of the topologies generated with nDNA and mtDNA are not significantly different from one another when tested against the mtDNA data set. In contrast, the nDNA-generated topology is significantly better than the mtDNA-generated topology when tested against the nDNA data, which suggests that there is no true conflict between the data sets.

Combining all data yielded a tree with the same topology as the nDNA data set, with very high support for a grouping of *H. japonicus* with the eastern Pacific species, and increased support for a sister relationship between *H. nipponensis* and *H. olidus* relative to the mtDNA and nDNA partitions (Fig. 5). After mapping the high (*) and low (+) scale-count groups onto the phylogeny, it was clear that the trans-Pacific species with similar scale counts were not monophyletic (Figs 4 & 5).

Analyses by individual gene partition produced several interesting results. First, it appears that 16S evolves too slowly to provide a good estimate of phylogeny for the timeframe of evolution of *Hypomesus*, as *H. pretiosus* and *H. transpacificus* individuals grouped as a polytomy, and support levels for other relationships were also relatively low in both ML and Bayesian analyses (data not shown). Furthermore, support for a monophyletic group of *H. japonicus*, *H. nipponensis* and *H. olidus* from the mtDNA phylogeny (Fig. 4) was evident in only the two most rapidly evolving gene regions, cyt*b* and the Bayesian analysis of ITS2 (although very poorly supported, posterior probability < 0.7). Analyses of S71 and RAG1 individually were generally concordant with the results of all data combined, although they supported a topology with *H. nipponensis* as basal to the rest of the species (data not shown). This topology also appeared in the set of trees generated from the Bayesian analysis of all the data combined, although at very low frequency, and was strongly supported by parsimony analysis [92% (nDNA), 83% (all DNA), 1000 bootstrap pseudoreplicates; data not shown, allDNA tree available in TreeBase, M3309]. Because of this uncertainty, we consider the placement of *H. olidus* as unresolved (see below).

Biogeographical scenarios

Shimodaira–Hasegawa tests comparing the molecular phylogeny (Fig. 5) with the expected topologies under each *a priori* biogeographical hypothesis (Fig. 2) showed that the molecular phylogeny is significantly better than McAllister's (1963) hypothesis of scale-count relationships (Fig. 2a), the *a priori* northern Pacific ancestor hypothesis (Fig. 2b) and the scenario of an eastern Pacific origin (Fig. 2c; $P << 0.001$ in all cases). For the eastern Pacific hypothesis, we also tested a constraint tree with *H. pretiosus* in the basal position as well as trees with *H. olidus* in between the two eastern Pacific taxa, with the same result. Comparison of the molecular topology (Fig. 4) with *H. nipponensis* and *H. olidus* as sister taxa to a tree with *H. nipponensis* basal to the rest of the species (Fig. 2d) showed no significant difference (–8096.7 vs. –8101.0, $P = 0.2$); therefore the position of *H. olidus* in the phylogeny of *Hypomesus* as either sister or derived relative to *H. nipponensis* remains uncertain. Taken together, the results of the SH tests suggest a western Pacific origin for *Hypomesus*.

Results from lagrange (Ree *et al.*, 2005) suggested a geographically more widespread ancestor (Fig. 6), although this analysis also supported a role for the western Pacific as a

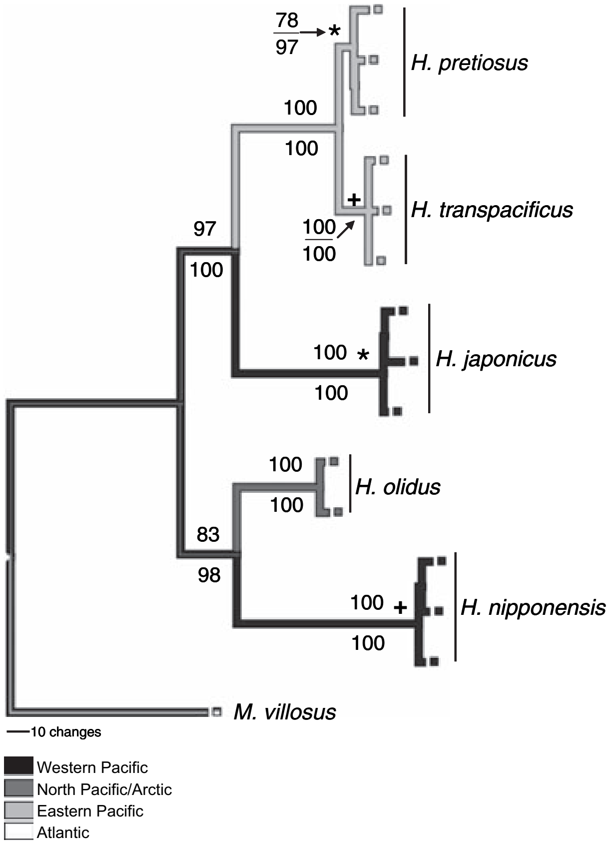

Figure 5 *Hypomesus* phylogeny from combined mtDNA [cyt*b* and 16S] and nDNA data sets [ITS2, S71 and RAG1]. *, +, Species with high and low lateral line scale counts, respectively; WPac, NPac, EPac, geographical distributions in the western, northern and eastern Pacific, respectively. Numbers above nodes represent bootstrap support values from 1000 pseudoreplicates in a maximum likelihood analysis; those below nodes are posterior probabilities from a consensus of 17,000 post-burn-in trees generated through Bayesian analysis (2×10^6 generations). *Mallotus villosus* is the outgroup. Geographical areas are mapped onto the phylogeny following the model described in Fig. 2.

centre of evolution for the group (see Discussion). Relatively high values of dispersal and extinction ($\lambda_D = 0.9$, $\lambda_E = 0.1$) yielded significantly more likely scenarios (likelihood ratio test, $P < 0.05$, d.f. = 4); therefore the other parameter combinations are not discussed further. The simulations allowing some dispersal across the Pacific produced similar results, but with a western Pacific and Arctic ancestor at node 1 and a western/northern Pacific and Arctic ancestor at node 2. Results from simulations where *H. olidus* was polymorphic for all areas were similar to those where *H. olidus* was restricted to the North Pacific and Arctic, except that the most likely scenario for the ancestor at node 2 (*H. olidus*–*H. nipponensis* divergence) was an ancestor present in all areas, and the ancestor at node 3 (*H. japonicus*–*H. pretiosus*/*H. transpacificus* divergence) had a distribution in the west, north and east Pacific (data not shown). Although these are the most likely scenarios, for all nodes apart from node 4 there were others that fell within two

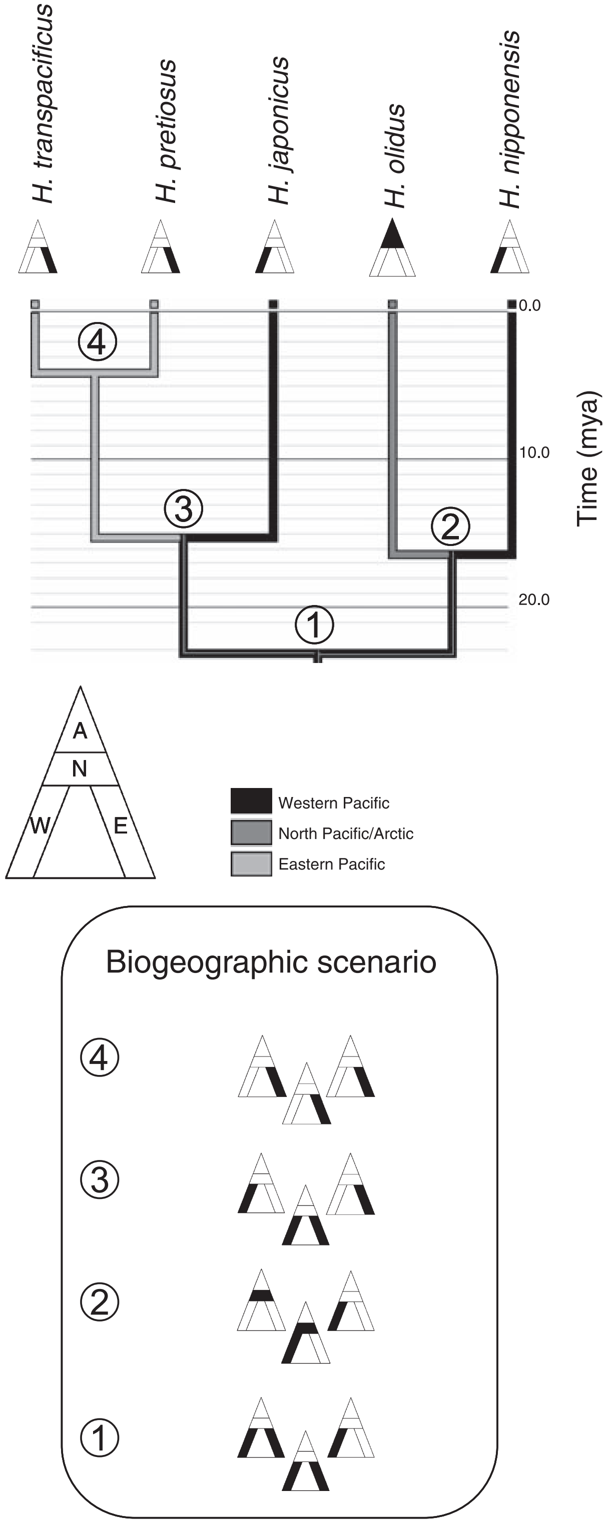

Figure 6 LAGRANGE maximum likelihood estimates of ancestral range and inheritance scenarios based on a model with a root node age of 22.9 Ma, no west–east Pacific dispersal, and relatively high rates of dispersal and extinction ($\lambda_D = 0.09$; $\lambda_E = 0.01$). Reconstructions with highest likelihoods are shown. Geographical areas are mapped onto the phylogeny following the model described in Fig. 2.

log-likelihoods of the most likely scenario. We attribute the multitude of scenarios to the small number of taxa in the phylogeny and relatively high amount of homoplasy (R. Ree, pers. comm., 2006). Further analysis in the context of an Osmeridae and/or Osmeroidea phylogeny may help clarify *Hypomesus* biogeography further.

Embiotocidae and *Sebastolobus* cyt*b* divergence

For a direct comparison with other trans-Pacific taxa, we identified two similarly distributed groups of fishes for which cyt*b* sequence data were available. Uncorrected pairwise cyt*b* sequence divergence in the Embiotocidae between the two basal western Pacific *Ditrema* and *Neoditrema* and the eastern Pacific *Hypselurus* were *c.* 14.7%, whereas in *Sebastolobus* the eastern (*S. alascanus*) and western (*S. macrochir*) Pacific species differed by *c.* 6%. This compares with uncorrected cyt*b* sequence divergence between the western Pacific *H. japonicus* and the eastern Pacific *H. pretiosus* and *H. transpacificus* of *c.* 10.5%.

DISCUSSION

Hypomesus phylogeny

Our well supported phylogeny from combined ML and Bayesian analyses of all five gene regions (Fig. 5) provides several key insights into *Hypomesus* evolutionary patterns. First, the apparent conflict in the placement of *H. japonicus* between the mt and nDNA phylogenies (Fig. 4) emphasizes the need for using multiple loci, both mitochondrial and nuclear, for inferring phylogeny. The sequence divergence between *H. japonicus*, *H. nipponensis* and *H. olidus* is large (10–14%, uncorrected cyt*b*) and speciation seems to have happened on a relatively narrow timescale relative to the divergence of *H. pretiosus* and *H. transpacificus* (*c.* 2.5%, uncorrected cyt*b*; Figs 4 & 5), which suggests that the only markers that show even a poorly supported relationship between these three species (cyt*b* and ITS2) may have reached a saturation point that obscures the phylogenetic signal. We interpret the differences between the mtDNA and nDNA phylogenies as a false conflict, and it is clear that if only the mtDNA gene regions had been included, a very different picture of the relationships within this genus would have emerged. Furthermore, analyses with all the data (Fig. 5) led to increased support values for all relationships relative to analyses by individual gene region (data not shown) and the mtDNA and nDNA partitions (Fig. 4), indicating that uncertainties within partitions are sometimes resolved when all information is combined.

One uncertainty that was not resolved by combining all data was the placement of *H. olidus* within the *Hypomesus* phylogeny. Although a sister relationship between *H. olidus* and *H. nipponensis* is apparently strongly supported (Fig. 5), an alternative topology with *H. nipponensis* as basal (Fig. 2d) could not be rejected statistically (see Results). Further, parsimony analysis supports a sister relationship between *H. nipponensis* and the rest of the *Hypomesus* species (83% bootstrap support, data not shown). This conflict is interesting as *H. olidus* has the widest distribution of all the *Hypomesus* species, with populations in both North Pacific and Arctic drainages (Fig. 1; McAllister, 1963). For the similarly distributed cisco (*Coregonus autumnalis*), populations from drainages in the Arctic Ocean differ from those further south in the Bering Sea in a number of morphological traits, to the extent that they are now considered separate species (*C. autumnalis* and *C. laurettae*) (McPhail, 1966; Eschmeyer, 2006). These two species are thought to have diverged in allopatry from a common ancestor distributed throughout the Arctic and Bering regions, whose range was divided by the formation of the Bering land bridge at the onset of the Pleistocene glaciations (McPhail, 1966). A similar north–south split has been suggested for the Dolly Varden char complex (*Salvelinus malma*: Behnke, 1980; Phillips *et al.*, 1999). Although the two populations of *H. olidus* that we sampled occurred on opposite sides of the Pacific (Fig. 1), we did not have information from populations in intervening areas (e.g. Arctic Ocean, Aleutian Archipelago) and, consequently, the uncertainty may result from a lack of data for this region. Additional sampling of Arctic populations may help clarify the position of *H. olidus* within the *Hypomesus* phylogeny and allow more direct comparisons with similarly distributed North Pacific taxa.

Regardless of the exact placement of *H. olidus*, it is clear from mapping the lateral line scale counts onto the phylogenies that species with similar counts are not monophyletic (Figs 4 & 5). Because the species groups based on these counts are not supported by the phylogeny of *Hypomesus*, our data suggest that scale-count phenotypes (high and low count forms) have evolved in parallel on each side of the North Pacific Ocean. Parallel evolution of phenotypes is a well documented phenomenon in many taxa (Losos *et al.*, 1998; Wiens *et al.*, 2006), and particularly in north temperate fishes (Behnke, 1972; Taylor, 1999). The difference in this instance is that lateral line scale counts are presumed neutral, whereas parallel evolution is usually associated with traits that evolve due to similar selective environments in different geographical regions (Simpson, 1953). Although less likely, parallel evolution in neutral DNA regions has been demonstrated as theoretically possible (Orr, 2005); however, the prevalence of this phenomenon in neutral traits in nature is unknown. Lateral line scale counts are used as identifying characters in taxonomic keys for a number of different fishes (Scott & Crossman, 1998). Although this trait may be useful for distinguishing species in the field, its utility as a systematic character can be known only through comparative phylogenetic analyses of different fishes. Recent work on rockfish (*Sebastes*) evolution has also shown parallel evolution of many traits (Hyde & Vetter, 2007). Mapping morphological characters onto well resolved phylogenies across multiple groups of fish would be informative in identifying both traits that are prone to evolve in parallel as well as those that are good indicators of evolutionary relationships.

Original classifications based on subspecies (McAllister, 1963) and scale-count groups (Klyukanov, 1970; Saruwatari *et al.*, 1997) that required two trans-Pacific relationships in *Hypomesus* (Fig. 2a) are not supported by the molecular phylogeny. There is, however, at least one trans-Pacific disjunction in the genus, that between *H. japonicus* and the two eastern Pacific species, *H. pretiosus* and *H. transpacificus* (Fig. 5; discussed below). Our finding that the two eastern Pacific species are sister taxa is in agreement with allozyme data (Stanley *et al.*, 1995; Trenham *et al.*, 1998) that showed *H. pretiosus* and *H. transpacificus* are more similar to each other than are *H. transpacificus* and *H. nipponensis*, which were formerly subspecies of *H. nipponensis* (McAllister, 1963). Our data also indicate a relatively recent divergence of the eastern Pacific species (Figs 4 & 5; discussed below).

Biogeography of *Hypomesus*

The paucity of fossil osmerids and the disagreement about extant osmerid relationships makes the formation of a plausible biogeographical scenario for these fishes particularly challenging. There are no fossil *Hypomesus*, and the oldest fossil osmerid dates to the Palaeocene and is postulated to be related to the Japanese ayu *Plecoglossus altivelis* (Wilson & Williams, 1991); however, the relationship of *P. altivelis* to other osmerids remains controversial (Johnson & Patterson, 1996 and references therein), preventing even rough calibration of an osmerid-specific molecular clock from these data. Although inconclusive, two reasonable rates of cyt*b* evolution are available: 0.5–0.9% per Myr for ectothermic vertebrates (Martin & Palumbi, 1993) and 1.56% per Myr for thornyhead rockfishes (Stepien *et al.*, 2000). To assess which of these rates may be most appropriate for *Hypomesus*, we calibrated a molecular clock based on the divergence of *H. japonicus* from *H. pretiosus* and *H. transpacificus* (Table 2) and the origin of the Sea of Japan in the Miocene around 15 Ma (Itoh *et al.*, 1997), under the assumption that the ancestor of *H. japonicus* evolved in this basin, an assumption that may be refuted or supported based on future fossil osmerid discoveries and/or further biogeographical analyses. This calibration yielded a rate of 1.77% per Myr. As this rate is close to the 1.56% per Myr recently proposed for rockfishes, we applied the range of these approximations to the corrected cyt*b* sequence divergence within *Hypomesus*. The cyt*b* and Bayesian estimates suggest that speciation events in *Hypomesus* are roughly associated with climatic changes in the Cenozoic (Table 2).

The results from LAGRANGE (Fig. 6) suggest a more complicated biogeographical history than the western Pacific origin obtained from the dispersalist approach (Fig. 2; SH tests in Results). In general, they suggest a scenario in which pan-Pacific or generally more widely distributed ancestors repeatedly underwent speciation following range fragmentation (Fig. 6). With *H. olidus* restricted to the northern Pacific and Arctic, the divergence between *H. olidus* and *H. nipponensis* is congruent with a hypothesis where a widespread ancestor had its range fragmented due to cooling temperatures in the mid-Miocene, with *H. olidus* inheriting the northern part of the range and then dispersing into the Arctic, while *H. nipponensis* evolved in the western Pacific (node 2; Fig. 6). The trans-Pacific divergence between *H. japonicus* and *H. pretiosus*/*H. transpacificus* occurred through a split within an ancestor that already had a disjunct distribution across the North Pacific (node 3; Fig. 6). This distribution may also have been inherited from the ancestor at node 1; however, it is possible that the lineage between nodes 1 and 3 underwent a range expansion to the northern Pacific that was divided before the divergence at node 3 (Fig. 6). The most recent speciation event (*H. pretiosus*–*H. transpacificus*) occurred in the eastern Pacific during the Pliocene or early Pleistocene (Table 2). *Hypomesus pretiosus* is found along the western coast of North America from Alaska to California, and *H. transpacificus* is endemic to the San Francisco estuary region of the Sacramento–San Joaquin River basin (Moyle, 2002; Fig. 1). These distributions, coupled with the estimated time (Table 2) and location of divergence (Fig. 6), suggest that a plausible speciation scenario involves a vicariant split of a widespread eastern Pacific ancestor when a population was isolated in a freshwater basin in western California. The extensive inland seas of the late Miocene had receded by the Pliocene (Oakeshott, 1978; Norris & Webb, 1990), which predates the estimated divergence time; however, the most recent glacial period is associated with drops in sea level, and it is possible that an ancestral population of these fishes was isolated in the series of Pleistocene lakes in the southern San Joaquin Valley (Norris & Webb, 1990), thereby leading to differentiation of the marine and estuarine species. Comparing divergence times of other apparent marine-derived species endemic to the Central Valley region of the Sacramento–San Joaquin basin, such as the Kern brook lamprey (*Entosphenus hubbsi*; Moyle, 2002), would clearly be of interest, although to our knowledge no such estimates are available.

Mapping the dispersalist model from Fig. 2 onto the *Hypomesus* phylogeny used for the LAGRANGE analysis shows that this approach yields a similar interpretation, although it supports a northern or western ancestor at nodes 1 and 3 (Fig. 6). Neither the LAGRANGE nor dispersalist model of *Hypomesus* supports the expectations depicted in Fig. 2; however, if *H. olidus* is given a widespread Pacific and Arctic distribution, the dispersalist model supports a western Pacific origin for the genus (data not shown). Further, although the most likely reconstructions for the root node in the likelihood framework is an ancestor with a western and eastern Pacific distribution, a western Pacific ancestor falls within two log-likelihoods; therefore a western Pacific ancestor for *Hypomesus* cannot be rejected.

Comparative biogeography of the North Pacific

Comparative biogeographical analysis invokes concordance in patterns of distribution across different taxa to support the role of large-scale geological events in shaping their evolutionary patterns (Lomolino *et al.*, 2006). In assessing concordance, two relevant questions are: what is the timing of the divergences, and what is the area of origin?

To address the first question on timing, Cenozoic cooling periods beginning in the mid-Eocene are thought to have led to diversification across a variety of taxonomic groups, with a large literature on fishes, molluscs and crustaceans in particular. A well preserved fossil record has allowed relatively accurate dating of species radiations in a number of molluscan (MacNeil, 1965; Titova, 1994; Oleinik, 2001; Amano & Vermeij, 2003) and crustacean (Schweitzer, 2001) taxa. Relatively early radiations in the Eocene and Oligocene epochs have been suggested for some gastropod (Titova, 1994) and decapod (Schweitzer, 2001) groups; however, much of the literature on North Pacific evolution has centred on the importance of the Miocene and, to some extent, the Pliocene, in generating diversity (Andriashev, 1939; Briggs, 1974). Cooling beginning in the mid-Miocene is thought to have been a particularly important evolutionary pump in a number of North Pacific taxa, including whelks (Collins *et al.*, 1996), periwinkles (Reid *et al.*, 1996), decapods (Schweitzer, 2001), kelps (Estes & Steinberg, 1988), and fishes such as poachers (Laroche, 1986), salmonids (Stearly, 1992) and rockfishes (Kai *et al.*, 2003). For fishes, early hypotheses for many groups emphasized the importance of climate and associated sea-level changes in the Plio- and Pleistocene epochs (Andriashev, 1939; Tarp, 1952; Lindberg, 1953 cited by Briggs, 1974; Neave, 1958), and more recently the possible role of tectonic events in promoting diversification, particularly in the eastern North Pacific, has been highlighted for the Pacific salmon genus *Oncorhynchus* (Montgomery, 2000).

Of particular interest in the current study was the phenomenon of trans-Pacific distributions. Although the original trans-Pacific sister relationships based on lateral line scale counts were not supported by our phylogenetic analysis, a trans-Pacific relationship was identified between the western *H. japonicus* and the two eastern species *H. pretiosus* and *H. transpacificus* (Fig. 5). Comparison of uncorrected cyt*b* distances between this *Hypomesus* disjunction (10.5%) and that in surfperches (14.7%) and thornyhead rockfishes (6%) shows that, if rates of molecular evolution are similar across these groups, the trans-Pacific divergences occurred during different time intervals. Our divergence estimates suggest a mid-Miocene divergence for the *Hypomesus* disjunction. Bernardi & Bucciarelli (1999) and Stepien *et al.* (2000) both estimated the divergence between their respective western and eastern taxa in the early Pliocene at *c.* 5 Ma, which clearly assumes different cyt*b* evolutionary rates (Stepien *et al.*, 2000 estimated the divergence based on control region sequence divergence). With the estimated rates of cyt*b* evolution, the trans-Pacific divergences in these three groups of fishes are apparently much older than the Pleistocene glaciations that have been thought responsible for generating many trans-Pacific relationships (Bernardi & Bucciarelli, 1999). The relative paucity of phylogenetic work on other pan- and trans-Pacific taxa that includes all species prevents additional comparisons, although Kai *et al.* (2003) and Hyde & Vetter (2007) showed that early hypotheses of several trans-Pacific sister relationships in the rockfish genus *Sebastes*, based on morphological analyses (Matsubara, 1943), are also unsupported by molecular analyses. Many studies of organisms with such distributions have contributed to Pacific–Atlantic or trans-equatorial relationships (Harrison & Crespi, 1999; Møller & Gravlund, 2003; Väinölä, 2003; Grant *et al.*, 2005) or have addressed questions focused on a more local scale (Johns & Avise, 1998). Additional molecular data for trans-Pacific sister taxa will allow future tests for simultaneous vicariance (Hickerson *et al.*, 2006) to assess whether Cenozoic climate changes resulted in the current distributions. Further, we are sensitive to the much-discussed problems with molecular clocks (reviewed by Arbogast *et al.*, 2002), possible problems of cyt*b* saturation, and uncertainty regarding the calibration point. Analysis within a larger phylogenetic framework, including the Osmeridae and Osmeroidea, where fossil calibration points are available, will allow additional confirmation, or refutation, of the biogeographical interpretations.

Incomplete geographical and/or taxonomic sampling also limits comparisons of ancestral area of origin. Our biogeographical analysis of *Hypomesus* suggests either a western Pacific or a pan-Pacific ancestor for the genus, depending on the reconstruction approach. Although often not tested in a phylogenetic framework, and in many cases still controversial, the western Pacific has been suggested as an important area of origin for a number of fishes, including *Oncorhynchus* (Neave, 1958), *Salvelinus malma* (Oleinik *et al.*, 2005), *Gasterosteus aculeatus* (Haglund *et al.*, 1992; Ortí *et al.*, 1994; Higuchi & Goto, 1996) and *Sebastes* (Barsukov, 1981; Hyde & Vetter, 2007), and many invertebrates (MacNeil, 1965; Titova, 1994; Oleinik, 2001). Furthermore, Gladenkov (1994) infers that from the Oligocene through the Neogene, trans-Pacific migrations of molluscan fauna appear to be more frequent from west to east than *vice versa*. Although the eastern Pacific has been supported as an area of origin for a number of other taxa [e.g. Embiotocidae (Tarp, 1952; Bernardi & Bucciarelli, 1999); Scorpaenidae (Briggs, 1974); *Nucella* (Amano *et al.*, 1993); *Littorina* (Reid *et al.*, 1996)], the relatively complex geological history of the western Pacific, with basins such as the Sea of Japan and possibly the Sea of Okhotsk undergoing periodic isolation (Lindberg, 1953 cited by Briggs, 1974; Zenkevitch, 1963), suggests that formation of such barriers has been an important mechanism for generating diversity in the North Pacific, including that in *Hypomesus*, under an allopatric model of speciation.

CONCLUSIONS

In this study we present a phylogenetic reconstruction of *Hypomesus*, a genus within a systematically problematic group of fishes, which showed that species-group designations based on lateral line scale counts do not reflect ancestry of the species. The placement of the widely distributed *H. olidus* is not yet resolved, although we expect that including samples of this species from Arctic drainages will help clarify its placement in the phylogeny and allow direct comparison with other

North Pacific/Arctic species. Our biogeographical analyses suggest an important role for the western Pacific, and ML reconstructions of ancestral ranges support the idea that Cenozoic climatic changes have been important drivers of diversification. Precise dating of divergences in *Hypomesus* is currently not feasible due to a lack of fossil information for these fishes, although best estimates strongly suggest they considerably pre-date the climate fluctuations of the Plio- and Pleistocene epochs historically thought to be responsible for generating trans-Pacific relationships in many fishes. The hypothesized time periods of *Hypomesus* diversification are implicated in divergences in a number of other similarly distributed North Pacific taxa, although the extent of comparison is limited due to a lack of phylogenetic data in many groups. Not surprisingly, it is often the western Pacific species that are missing, probably due to the difficulty of obtaining samples from many remote areas in this vast region. Along with Uschakov (1971) and Amano & Vermeij (2003), we view the North Pacific as an ideal arena for comparative biogeographical work and encourage trans-Pacific collaboration whenever possible. Accumulation of phylogenetic and biogeographical data on pan-Pacific taxa will facilitate comparisons of both timing and area of divergences within the North Pacific Ocean.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online:

Appendix S1 Voucher numbers and sample localities.

Appendix S2 GenBank accession numbers.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2699.2007.01782.x

BIOSKETCHES

Katriina L. Ilves is a PhD candidate working on systematic and biogeographical questions concerning the Northern Hemisphere smelt family Osmeridae, in the Department of Zoology at the University of British Columbia. Her research interests include biogeography and evolution of fishes, conservation and natural history collections.

Eric B. Taylor is a Professor of Zoology and an Associate Director of the Biodiversity Research Centre at the University of British Columbia. His research interests include vertebrate population genetics, zoogeography and the ecology and genetics of speciation. He is also a member of the Native Fishes Research Group, which focuses on the study and conservation of native fishes of British Columbia.

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