Title: Investigation of the trophic ecology and flexibility of larvae sardine and anchovy, its relationship to growth, feeding opportunities and recruitment success, and implementation in stock assessment.

Principle Investigator: Andrew R. Thompson

Principle Investigator Institution: NOAA NMFS SWFSC, Fisheries Research Division (FRD)

Research priorities: Our project addresses the following FATE research priorities: **1.** Studies that develop indices of environmental and oceanographic indicators, test hypotheses, or evaluate analytical tools to investigate specific mechanisms driving interactions between fisheries and climate and environmental drivers of managed species. Vital rates and parameters of interest include: recruitment, growth, distribution, trophic ecology, natural mortality, health, and habitat availability. Such studies should directly improve stock assessments via explanation and/or prediction of variability in the above population processes. Of particular interest are studies for California Current Clupeids; and **6.** Explore the feasibility and evaluate the utility of incorporating climate/environmental/oceanographic indices into stock assessment models. Identify how environmental indicators can supplement or be considered alongside stock assessment output and how environmental and climate forecasts can be incorporated into stock assessments.

Project Duration: 2 year, FY 2015-2016

Total Funding Request: $127,900

Year 1 Request: $79,400**; Year 2 Request:** $48,500

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List Institutional Breakdown of Year 1: $79,400 to SWFSC

List Institutional Breakdown of Year 1: $48,500 to SWFSC

Background

Even before the impact of commercial fishing Pacific sardine (*Sardinops sagax*) and Northern anchovy (*Engraulis mordax*) populations exhibited large fluctuations [1]. Both species have collapsed and resurged numerous times over the past two millennia, likely in response to oceanographic changes [2,3], and wide swings in recruitment success are evident over the past 30 years (Fig. 1). Environmental factors that have been related to sardine or anchovy recruitment or population size include water temperature, the Pacific Decadal Oscillation (PDO) index, mesoscale eddies and fishing pressure [e.g., 2,4-6]. However, with the exception of fishing, these factors likely affect recruitment indirectly by, for example, impacting the availability and/or spatio-temporal overlap with suitable prey. Further, despite decades of research seeking to elucidate the causes of these population fluctuations, the ultimate mechanism(s) governing the variability are not resolved. **Given the uncertainties surrounding the specific mechanisms impacting recruitment, and their interactions with one another, it is necessary to elucidate the precise environmental factors that affect sardine and anchovy population dynamics**.

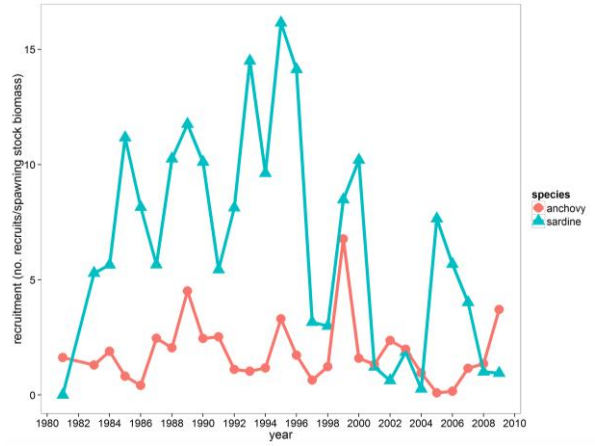

Fig. 1: Recruitment success of Pacific sardine (blue) and Northern anchovy (red) in the California Current Ecosystem over the past three decades.

Many studies have examined the effects of physical factors such as temperature, salinity, mesoscale features and water flow on sardine and anchovy recruitment [7-10], and the Pacific sardine harvest rule is one of the few management strategies in the world that considers temperature in its calculation of the fraction of the stock biomass that can be harvested each year [Pacific Fishery Research Council 11]. Specifically, Pacific sardine maximum sustainable yield drops from 15% to 5% of the total sardine biomass when mean sea surface temperature (SST) for a given year drops below 16.8° C. However, recent research suggests that SST is actually correlates poorly with sardine recruitment [12]. Therefore, additional environmental parameters need to be considered to better manage this stock. In particular, it would be beneficial to determine if diet composition affects sardine recruitment. Moreover, recent population trends suggest that sardine may be entering a prolonged period of low population size while anchovy abundances may be increasing [13]. Therefore, although anchovies are not currently actively managed, it is likely that formal stock assessments will need to be conducted for both anchovies and sardines in upcoming years. There is thus critical need to elucidate how direct environment factors affect recruitment success of both species. **The aim of this proposal is to better inform stock assessment and/or harvest rules of sardine and anchovy by evaluating the effect of diet composition on growth and recruitment of these fishes.**

Recruitment variability is generally considered to result from complex trophodynamic and physical processes that affect growth and survival during early life history stages [14]. For sardine and anchovy within the California Current Ecosystem (CCE), processes operating at the late larval or juvenile stage are thought to be the most important in regulating recruitment [7,15]. Feeding success early in life is crucial as starvation reduces growth and increases mortality [16,17]. Slower growth leads to longer periods of exposure to predation and reduces larval escape capabilities [18]. These processes likely explain a considerable proportion of the large fluctuation in recruitment and population size found in most species of fish [16,17]. Indeed, Rykaczewski and Checkley [19] hypothesized that changes in prey size structure resulting from upwelling variability affects sardine recruitment success in the CCE. However, little is actually known about the diet, prey preference and trophic ecology of sardine and anchovy larvae in this system [20]. Zooplankton community structure has been shown to be impacted by environmental forcing over inter-annual and decadal scales [e.g., 21,22] over which sardine and anchovy population size and recruitment have fluctuated. Therefore, **it is necessary to directly examine the feeding ecology of sardine and anchovy larvae to determine if changes in diet affect recruitment**. Notably, changes in food habits were observed in larval sablefish with changing environmental conditions [23] and in growth rates of Northern anchovy [24], and therefore it is likely that other species are also affected.

Fish larvae are selective in their feeding [25] both in terms of prey size and taxon composition [26]. Therefore, studies attempting to relate prey abundance to larval abundance, mortality, vital rate or recruitment need to consider only the fraction of the prey community that the larvae are actually feeding on. **Limited knowledge on the feeding preferences, flexibility, long term feeding history and their effects on vital rates is likely the reason why so few studies have successfully linked fish recruitment fluctuations to changes in prey community composition** [27]. One reason that the diet-recruitment link has not been more fully investigated is that obtaining accurate diet information from wild larvae or juveniles has traditionally been very difficult or impossible. The high species richness of prey such as copepods within the CCE, where several species overlap in size and morphological characteristics, makes stomach content analysis problematic. Furthermore, microscopic methods of stomach content provide only a snapshot of the period between ingestion and digestion and therefore can fail to identify long-term consumption patterns [28]. Another reason why few studies have looked into the effects of prey availability is that, until very recently, few mesozooplankton samples from the CalCOFI 65-year time-series had been analyzed at a high degree of taxonomic resolution. In addition, the relatively coarse mesh sized nets (150-550 µm) that have been used for zooplankton sampling in the CalCOFI program may also fail to account for the abundance of small nauplii and protozooplankton which are important prey items for sardine and anchovy larvae [29]. Therefore, **in the proposed project we plan to investigate the feeding history of late larval stages of sardine and anchovy by stable isotope analysis on ^{15}N**. This largely eliminates the need for the expensive and time consuming work of identifying and measuring zooplankton *in situ* and in the larval stomach content.

The importance of heterotrophic protozoans in marine food webs was described in the early 1980s with studies of the microbial loop [30]. Protozoans are key grazers on phytoplankton [31] and are in turn preyed on by mesozooplankton [32]. Despite their potential importance as a food source for zooplankton, and the past 100 years of knowledge that fish larvae also eat protozoans **only a few studies have directly evaluated the importance of protozooplankton on ichthyoplankton diet, growth or survival** [33]. However, the few studies that have studied this topic reported that protozoans account for a large part of the diet in the earliest stages of Northern anchovy (*Engraulis mordax*) larvae [34,35], larval cod (*Gadus morhua*) [36] and other fish species [37-40]. This lack of focus is due to the fact that many diet studies focus on microscopic gut content analysis, which typically fail to identify soft-bodied protozoans that degrade much faster than crustaceans. Moreover, such studies require multi-disciplinary work on microbial, plankton and fish ecology that combine traditional methods with new biochemical, molecular and microscopic tools. Hence, prey availability to first feeding larvae may have been consistently underestimated as most previous research focused on crustacean plankton in larval diets [33]. **We will utilize a newly developed method that uses Compound Specific Isotopic Analysis on Amino Acid (CSIA-AA) to account for the role of protozoans in larval feeding** (see method)**.**

Larval condition and growth depends on the quantity and quality of prey, but the availability of prey is dependent on the trophic flexibility of the larvae. Theoretically, under optimal feeding conditions, the trophic niche width of larvae at size should remain constant [41], while in poor feeding conditions niche width should increase in order to compensate for lack of food [42]. Indeed, recent studies show that some larval species can switch diet to other prey taxa [26,43-45] or trophic levels in response to changes in the zooplankton community, and that larval growth performance varies with prey species [46, see Fig. 2]. Fishes **with greater trophic flexibility may be less sensitive to changes in their feeding environment** [44,45]. In the proposed project **we will study the relationship between the trophic position and niche width in larval sardine and anchovy, and its relationship to growth and recruitment**.

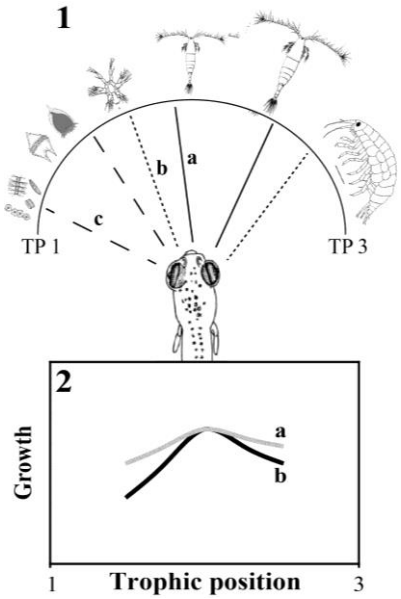

Fig. 2: 1) Illustration of two species that differ in their trophic flexibility (a and b) or trophic niche (c), and 2) of two species that are differently adapted to feeding on lower/higher TP in terms of growth.

Approach

The overarching goal of this project is to determine if the trophic ecology of sardine and/or anchovy larvae can help us better understand why growth and recruitment varies among years. We will focus on the California Current Ecosystem, which is an ideal model system for assessing the proposed objectives due to the wide array of physical and biological conditions it encompasses. In addition, this area has been thoroughly surveyed for the past 65 years by the CalCOFI (California Cooperative Oceanic Fisheries Investigations) program. CalCOFI has systematically collected oceanographic (e.g., ctd) and biological (e.g., oblique bongo tows where replicate plankton samples are preserved in ethanol and formalin) data on a quarterly basis within Southern California (Fig. 3). We will utilize CalCOFI samples for this research.

The objectives (see below) will be achieved by applying stable isotope analysis, the newly developed CSIA-AA method, and otolith analysis to anchovy and sardine larvae from CalCOFI samples to determine: i) trophic level variability of larvae in relation to environmental conditions; ii) the relationship between trophic position and larval growth performance, and iii) the role of protozoans in larval feeding ecology. **These results will then be used to determine the trophic niche and flexibility of larval sardine and anchovy, accounting for the intermediate protozoan trophic step. We will then determine whether growth and recruitment fluctuations of these two species are linked to changes in feeding conditions and larval trophic flexibility. If we find that there is a significant effect of diet properties on recruitment, we will evaluate how feeding condition can better inform sardine and/or anchovy harvest rules and stock assessments.**

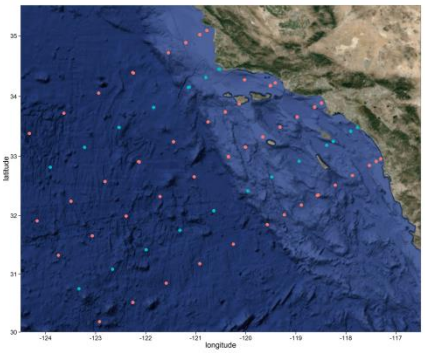

Fig. 3: Locations of CalCOFI stations off the coast of Southern California. Blue points depict stations from lines 80 and 90 where zooplankton assemblages have been fully characterized.

Method – The trophic position (TP) of larval sardine and anchovy will be estimated by Compound Specific Isotopic Analysis of individual Amino Acids (CSIA-AA). Enrichment of the ^{15}N isotope occurs in some AA's (trophic AA's, typically glutamic acid) while no enrichment occurs in others (source AA's, typically phenylalanine). The difference between the two AA's increases at a constant rate for each increasing trophic level within the food chain, making it possible to determine the TP of an organism. This method has previously been used to successfully document changes in trophic conditions with changing environmental conditions [47] and to determine the trophic position of fish [48,49]. The advantages of this technique are that: 1) TP can be estimated from two AA's in a single organism, 2) it reflects an integrated value of autotrophs that has actually been consumed in the studied food web, 3) it can be applied to formalin samples from historical collections and 4) it is more sensitive that traditional bulk ^{15}N analysis [48,50]. **New advances made by Prof. Michael Landry's lab at SIO using the trophic AA alanine has made it possible to account for the role of protozoans, which until now has been largely invisible in food web studies using isotopic methods** [51]**.**

Bulk isotopic measurements of ^{15}N enrichment in fish larvae in relation to the phytoplankton base of the food web will also be performed. This is a faster, low-cost method relative to the CSIA-AA that is useful to pinpoint samples of interest and allows for comparison of the two estimates.

The growth performance of the larvae will be determined by analysis of the sagitta otoliths from ethanol-preserved larvae. Individual growth increments will be counted and their width measured under microscope. Growth increments are deposited daily in the selected species during their early life, thus allowing for accurate age determination used to determine larval size at age [52,53]. Furthermore, otolith analysis will yield estimates of the larval growth history inferred by the width of the individual otolith growth increments.

A potentially confounding factor that could impact the relevance of our results to management is that sardine in southern California are thought to be comprised of northern and central stocks [54,55]. Specifically, the northern stock spawns when SST is between approximately 11°C and 17°C while the central stock spawns between 17 and 25°C [54]. Although sardine in southern California are usually mostly comprised of individuals from the northern stock, the central stock may migrate north from Mexico when SST exceeds 17°C off California

(typically during summer and fall). Because US sardine management focuses on the northern stock, we will limit our analysis to the northern stock by utilizing samples only from winter and spring in locations where SST is < 17°C.

We will utilize these methods to address the following three objectives:

***Objective 1*: Determine the relationship between zooplankton assemblage composition, larval trophic position and growth**. Diets are known to differ between anchovy and sardine larvae [29]. Changes in zooplankton community structure can alter the feeding opportunities of the two species and alter their trophic position. Consuming smaller prey, typically from a lower trophic level that contains less energy, requires more energy expenditure while handling the prey. Larger, energy-rich prey from higher trophic levels has a lower catchability and thus requires more energy spent on prey searching. Hence, **we hypothesize that: sardine and anchovy larvae at size differ in their trophic niche and flexibility; that changes in the composition of prey available to the larvae affects their trophic position; that growth is reduced in larvae feeding on relatively lower and higher trophic levels; and that protozoans contribute significantly to the larval diet of both species (Fig. 2).**

Although zooplankton taxonomic resolution is generally lacking for CalCOFI samples, mesozooplankton size and taxonomic composition and protozoan abundance from stations on CalCOFI lines 80 and 90 (Fig. 3) in winter and spring between 2004 and 2014 have been quantified and made available by Mark Ohman and Mike Landry's laboratories at SIO. To evaluate how zooplankton assemblages differ among years we will perform a Nonmetric Multidimensional Scaling (NMDS) analysis and Analysis of Similarity (ANOSIM). We will then select three or more groups of stations where zooplankton assemblages are similar within groups but significantly different among groups. Next, we will select ten ~20 mm larvae from ethanol-preserved samples (or the maximum number available if there are less than ten) for each species from each group to be analyzed for bulk ^{15}N content at the Analytical Facility at SIO (n = approximately 180 larvae). These larvae have already been removed from the plankton samples and are immediately ready to be used for this analysis. Concurrent phytoplankton samples are available at SIO from these years and will be analyzed to determine baseline ^{15}N values at the bottom of the food web, allowing for estimation of the larval TP. Stations where larvae differ in TP will be selected for further in depth CSIA-AA (allowing for more accurate TP estimation) and otolith analyses. Effects of changes in prey community composition on larval TP will be investigated by PERMANOVA analysis. The impact of TP and other available environmental factors such as SST, salinity, mixed layer depth, chlorophyll *a* on growth will be tested by multiple nonlinear regression or GAM analysis.

Validation of enrichment of AA's in larval fish feeding on protozoan prey will be acquired through a feeding experiment in another project at SIO by Swalethorp financed by the Danish Council for Independent Research (DFF). This experiment will also seek to develop a new trophic enrichment factor (TEF) for alanine in fish to calculate their TP accounting for intermediate protozoan trophic steps. If enrichment of alanine is specific to protozoans, then the difference between alanine and glutamic acid based estimates would distinguish dietary contribution from the protozoan trophic pathway and mesozooplankton prey. This work will be well underway or completed by June 2015, when the research in this proposal, if funded, will commence.

***Objective 2*: Assess the temporal stability of the larval anchovy and sardine trophic position**. **We hypothesize that the TP of the larvae differs between strong and weak recruitment years as a result of variable feeding conditions.** To address this objective, we will utilize formalin-preserved fish larvae (~20 mm length) from the CalCOFI 65-year time-series (all samples are currently sorted and ready for immediate use). We will select at least five strong and five weak recruitment years for this analysis. Fifteen larvae from each species collected at 3 stations within the center of the spawning area for each species in a given year. The spawning center will be identified by calculating the weighted mean coordinates of the center of sardine and anchovy egg distributions (this data is also currently available) using the aspace package in the statistical program R. Prescreening of the larval ^{15}N signature will be done by bulk measurements (5 replicates, 3 stations, 10 years, 2 species, n = 300 larvae). If some changes in ^{15}N are observed with the stable isotope analysis, we will also conduct more in depth CSIA-AA analysis (n = 300 larvae). As historical phytoplankton samples are not available for the entire 65-year time-series, source AA's will also provide baseline ^{15}N measurements for later calculation of TP from the bulk measurements. The plausibility of multiple GAM models that relate recruitment to TP and

other available environmental parameters (SST, salinity, mixed layer depth, chlorophyll *a*, zooplankton biovolume) will be assessed using Akaike Information Criterion adjusted for small sample size and cross validation.

***Objective 3*: Utilize TP to inform sardine and anchovy management.** An important area of uncertainty in stock assessment is determining recruitment strength for recent years (i.e., now-casting), and at present the sardine assessment utilizes a Beverton-Holt model to relate spawning stock biomass (SSB) to recruitment. Unfortunately, the SSB-recruitment relationship is rather weak for sardine and anchovy. Further, although some environmental parameters (SST, chlorophyll a, sea surface height) can accurately predict anchovy and sardine spawning locations [54,56,57], the relationship of these variables with recruitment success are tenuous, and the use of SST in the harvest rule for sardine has been recently debated. Therefore, the accuracy of sardine assessments could improve greatly if a factor that accurately predicts recruitment success is added to the stock assessment model. If our results show that there is a significant relationship between TP and recruitment, we will work to develop a TP time-series and potentially incorporate this index directly into the stock assessment as a predictor of recruitment. In addition, we will determine if TP outperforms SST in predicting sardine recruitment and evaluate whether TP could replace or augment SST in the sardine harvest rule. Because the dietary analyses can be done relatively rapidly, TP could be used to now-cast recruitment for a given year or forecast recruitment in the year following plankton collection. Thus, TP could be utilized to help estimate stock size and establish harvest rules in real time.

Timeline

The project will be carried out together with a FATE-funded research technician and in collaboration with Professors Mark Ohman and Michael Landry at Scripps Institution of Oceanography (SIO). All isotopic data will be generated during the first year (6/2015-6/2016) of the project when the technician will be available to assist with laboratory work. The second year (7/2016-6/2017) will be dedicated to analysis, writing manuscripts for peer-reviewed, scientific journals, and presenting results at meetings.

Benefits

Studies of the trophic ecology of fish larvae with changing environmental conditions; as well as the flexibility of individual species and its effect on growth are essential to predict changes in marine ecosystem structure. Nevertheless, fundamental understanding of fish larvae trophic ecology is still scarce. For instance, studies have only recently shown interest in resolving the protozooplankton – ichthyoplankton link, despite the potential importance of this trophic link in marine food webs. The proposed project seeks to provide significant advances in this area, and to show the **benefits of multidisciplinary approaches** using biochemical, morphological and environmental analysis methods to understand ecological processes. The anticipated results will provide new and valuable **insights into food web dynamics** through the identification of trophic relationships and new knowledge on how fish larval species differ in their ecological functioning.

This study will elucidate the relationship between the trophic ecology of two managed *Clupeid* species and recruitment variability within the California Current Ecosystem. Specifically, we will explorer linkages between prey community structure and the trophic niche and flexibility of late larval stages of Pacific sardine and Northern anchovy, and how it relates to growth performance. Furthermore, we will account for the role of protozoan trophic pathways in larval trophic ecology which is largely unknown and has barely been considered in fisheries models. Finally, we will evaluate if the trophic position of sardine and anchovy larvae in combination with different environmental parameters can explain the variability in recruitment observed in the CalCOFI surveys. If so this information will be incorporated into a new environmental index to improve stock assessment by better predicting sardine and anchovy recruitment.

Deliverables

- Provide managers with a novel indicator to predict sardine and anchovy recruitment strength that can be incorporated into stock assessment models
- Provide a method to account for protozoan trophic pathways in fish larval trophic ecology
- Prepare multiple scientific manuscripts to be published in peer-reviewed journals
- Present results at domestic or international scientific meetings

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