Introduction
The objective of the GLOBEC multinational programme, OFCCP (Oceanic Fisheries and Climate Change Project) is to investigate the effect of climate change on the productivity and distribution of oceanic tuna stocks and the fisheries for them in the Pacific Ocean, with the goal of predicting short- to long-term changes and impacts related to climate variability. One of the four main focus areas relevant to OFCCP’s objective is studies of the trophic structure in pelagic ecosystems.

Pelagic open-ocean ecosystems support important fisheries for tunas and other upper-level predators in all the world’s oceans. These fishes are wide-ranging, generalist predators with high energy requirements, and as such, are key components of the ecosystems. Ecological relationships among large pelagic predators, and between them and animals at lower trophic levels, are not well understood. Given the need to evaluate the implications of fishing activities on the underlying ecosystems, it is essential to acquire a reliable understanding of the trophic structure in these vast ecosystems (Fig. 1).

Knowledge of the trophic ecology of predator fishes has historically derived from diet studies. Stomach contents however, provide only a relative snapshot of the most recent meal at the time of day the animal is captured and under the conditions required for its capture, and can under-represent organisms that are digested quickly. Stable isotopes of carbon and nitrogen, on the other hand, integrate information on all components of the diet into the animal’s tissues. Stable C and N isotopes are used with increasing frequency for determining trophic interactions among consumers, and for tracking energy or mass flow through the trophic pathways of ecological communities (Fig. 1). This technology is only now being applied in pelagic marine systems that support tuna production.

In order to develop consistent strategies for stable isotope analysis (SIA) and consistent interpretation of the data, a workshop was held under the auspices of OFCCP Theme 2, Food Web Structure in Pelagic Ecosystems. The workshop on “Stable Isotopes in Pelagic Ecosystems” was held from 31 May–1 June 2004 in La Paz, Baja California Sur, Mexico. It was sponsored by GLOBEC; by the Pelagic Fisheries Research Program (PFRP), University of Hawaii; and by the Centro Interdisciplinario de Ciencias Marinas (CICIMAR), La Paz, Mexico. The workshop was a joint activity with Working Group 3 (Trophic Pathways in Open Ocean Ecosystems) of a new GLOBEC regional programme, CLIOTOP (Climate Impacts on Oceanic Top Predators). CLIOTOP has similar objectives as OFCCP, in terms of studying the trophic ecology in pelagic food webs, but the former focuses on comparisons within and between ocean basins worldwide and the latter focuses on comparisons within the Pacific Ocean. At the conclusion of the workshop, a brief business meeting concerning future OFCCP and CLIOTOP activities was held.

The workshop was attended by 27 participants from 5 countries. It was designed to review some of the current stable isotope studies in pelagic ecosystems, to present and compare current methods of SIA, and to exchange ideas on the interpretation of stable isotope data. Studies from the pelagic western, central, and eastern Pacific Ocean, eastern Australia ecosystem, eastern tropical Atlantic, and western tropical Indian Ocean were examined. In addition, studies in more localised areas in the Pacific Ocean, including the Hawaiian Islands, southern Baja California, and the Gulf of California, were represented. The long-term goal is to promote inter-ecosystem

Figure 1. Simplified food-web diagram of the pelagic ecosystem in the tropical eastern Pacific Ocean. The numbers inside the boxes indicate the approximate trophic levels of each group.
comparisons of pelagic food-web structure in the Pacific (OFCCP) and in the Pacific, Atlantic, and Indian Oceans (CLIOTOP) so that top-down (fisheries, predators) and bottom-up (climate) forces are accurately depicted in ecosystem models.

Background

Naturally-occurring stable isotope ratios in animal tissues have been used to reconstruct diets, to trace movements, and to track sources of carbon in the food web. Isotope ratios are expressed as δ13C and δ15N, which are the normalized 13C/12C and 15N/14N ratios of samples to standards, in parts per thousand (%). Isotopic fractionation of C and N takes place during metabolic processes, with the lighter isotope of each pair differentially excreted relative to the heavier isotope. Nitrogen isotope ratios are often used to estimate trophic position because the δ15N of a consumer is typically enriched by 3–4‰ relative to its diet (Fig. 2).

Isotope tracers in an animal’s tissues reflect not only what an animal eats, but also the environment the animal inhabits and the pollutants that are bioaccumulated. “Residents” should have an average chemical profile that is in equilibrium with the food and water of a home region, while “migrants” are isotope deviants (statistical outliers) from an average profile.

Project overviews

Several participants presented overviews of current projects that apply stable isotope analysis to detect ecological pattern in pelagic marine ecosystems. Three large-scale studies are being conducted in the Pacific, Atlantic, and Indian Oceans. A three-year multinational project, funded by the PFRP, is designed to define the trophic structure, establish an isotope-derived biogeography, and characterise large-scale tuna movements in the pelagic western, central, and eastern tropical Pacific. The project incorporates diet analysis, SIA, and food web modelling. Stomach, muscle, and liver samples are taken from a variety of predator species by observers on tuna fishing vessels, and particulate organic matter (POM), zooplankton, and prey organisms are collected on research cruises.

A component of the THETIS Project (Thons tropicaux écosystèmes), funded by IRD, France, is a study of regional characteristics of pelagic food webs, foraging strategies of top predators, and the influence of climate variability on the spatial distribution of fisheries in the eastern tropical Atlantic and the western tropical Indian Oceans. The studies include diet analysis, SIA of predators and their stomach contents, acoustic surveys of tuna forage, and modelling. Sampling of POM, filter-feeders encrusted on oceanographic buoys, and principal prey taxa are also conducted.

A large-scale ecosystem study by CSIRO, Australia, is being expanded with the objectives to identify the main ecosystems of the eastern tuna and billfish fishery (ETBF); to define the trophic structure within these ecosystems with emphasis on the relationship between target, bycatch, and threatened and protected species; to develop quantitative and qualitative models of the ecosystem/s; and to compare the ecosystem/s that underlie the ETBF with those of the warm and cold pools of the equatorial Pacific Ocean. Methods include trophic studies using gut content analysis, SIA, feeding behaviour and modelling.

Two studies that are being conducted by Ph.D. students at CICIMAR, La Paz, Mexico, using SIA were discussed. A study of the influence of environmental and geographic variability on the trophic structure of the cepopods and other zooplankton taxa over a broad region of the eastern tropical Pacific (ETP), using stable C and N isotopes, began in 2004. Another study incorporates diet analysis and SIA to infer feeding relationships among yellowfin tuna (Thunnus albacares) and two species of dolphins (spotted Stenella attenuata and spinner S. longirostris) in the ETP.

Two research professors at CICIMAR presented studies that are focused in regions off Baja California Sur (BCS) and the Gulf of California. A study of the trophic variability of sharks off BCS, as inferred from diet analysis and SIA, is in progress. The shark project is the source of data for the theses of four MSc students and one PhD student at CICIMAR. Another CICIMAR professor reviewed the results of a diverse group of completed research on sediments, sea lions, and sperm whale-jumbo squid trophic relationship, using stable isotopes of C and N.

Factors that affect variability in stable isotopes

Inter-ecosystem comparisons require that like tissues are used for SIA. Red muscle samples of yellowfin tuna from the Atlantic were significantly lighter in δ13C (by about 0.9‰) and heavier in δ15N (by about 0.7‰) than white muscle samples. Previous studies have shown that within each tissue type (e.g. white muscle), the isotope values are generally consistent throughout the body, but for bigeye tuna (Thunnus obesus) in the western Pacific and yellowfin tuna in the Atlantic, the isotope contents of white muscle from several body loci showed average within-fish variability of 0.5 and 1.0‰ for δ13C and δ15N, respectively. More work is needed to reliably compare within-species stable isotope values of white muscle in the anal area of longline-caught tunas with those of the dorsal musculature of purse-seine caught fish.

Preliminary stable isotope data show considerable within-school variability for the tropical tunas. The expected degree of variability for fish that remain in persistent schools and eat a uniform diet, based on previous studies of snappers, is 1.0–1.5‰ for both δ13C and δ15N. If within-school variability exceeds 1.5‰, the fish comprising the school were likely
feeding together only very recently. The following considerations may contribute to within-school differences in stable isotope composition. Schooling may be a highly dynamic process. In contrast to diet data, which typically show that tunas from the same school feed uniformly, stable isotopes suggest that tunas caught together often have different feeding histories, which suggests considerable mixing. Individual variability in feeding behaviour, nutritional condition, and size can contribute to within-school variability in stable isotope composition. Tunas feed on deep-dwelling prey to varying degrees, and mesopelagic prey typically have elevated δ¹⁵N content relative to epipelagic prey (see next section). Starvation results in elevated muscle δ¹⁵N due to deamination of the amino acids that make up body proteins. Body size often correlates with increasing stable isotope ratios because larger predators are capable of eating larger prey at higher trophic levels. Some preliminary data presented at the workshop showed this trend, and other data showed contradictory trends, or no trend, with size.

Food web implications

Comparisons of the stable isotope contents of tunas and their typical prey, determined by diet studies, often show a discrepancy in expected isotope enrichment. Average isotope enrichment is expected to be 3.4‰ and 0.7‰ per trophic lever for δ¹⁵N and δ¹³C, respectively, based on published literature reviews. This discrepancy may imply that some components of the diet are typically not observed in the stomach contents, perhaps prey eaten at night or small prey that are digested quickly.

The tissues of mesopelagic fauna typically have higher δ¹⁵N than those of epipelagic fauna due to changes in the δ¹⁵N of POM and prey items at these depths. Because of fractionation during deamination of amino acids, zooplankton release low-δ¹⁵N ammonium, causing their bodies and faecal pellets to be enriched in δ¹⁵N. These faecal pellets represent an important mechanism of export of high-δ¹⁵N nitrogen via POM from the surface ocean to mesopelagic depths (Fig. 3). In general, the data demonstrate that predators that feed deeper in the water column (e.g. bigeye tuna) tend to have higher δ¹⁵N values than those that feed in the upper mixed layer (e.g. yellowfin tuna) (Fig. 3). Deep-dwelling fishes like, opah (Lampris guttatus), blue shark (Prionace glauca), and lancetfish (Alepisaurus ferox) had higher δ¹⁵N than yellowfin and skipjack tuna (Katsuwonus pelamis) in waters off New Caledonia. Using stable N isotopes to better understand the bottom-up trophic connections leading to the diverse suites of predators in pelagic ecosystems requires simultaneous isotope analyses of the predators and the base of the various food webs.

Lipid effects on stable isotope analysis

Variable lipid contents of tissues can result in variations in δ¹³C values. For example, muscle is composed mostly of protein, while lipids are depleted in ¹³C relative to protein (by about 4–7‰). No standard protocol yet exists to determine whether lipids should be extracted before SIA or whether mathematical adjustment using the C/N ratio is adequate. A mass-balance equation is used to adjust δ¹³C measurements when lipid is not extracted, and its use was recommended only if C/N exceeds 4.8.

Implications of tissue turnover rates on stable isotopes

The isotopic composition of any given organism often depends on the type of tissue analysed. Due to different metabolic rates of different tissues, tissue turnover is variable, and this affects the isotopic composition. Isotopic turnover rates in yellowfin tuna are being analysed at the Hawaii Institute of Marine Biology. A two-pronged approach is used: a naturally-occurring diet shift by juvenile yellowfin in nearshore waters of Hawaii, and an experimental diet shift using captive yellowfin tuna. The tissue turnover rates were of the order of those of mammals and birds, higher than those of ectothermic fishes. The experimentally-measured turnover rate of liver was considerably higher than that of white muscle, which suggests that it is technically feasible to distinguish resident and migrant yellowfin tuna in nature using stable isotopes.

Common priorities of projects that address OFCCP and CLIOTOP objectives

In an effort to develop consistent strategies involving the application of stable isotopes in pelagic ecosystems, and to promote links between new and existing research projects and GLOBEC programmes, the following list of priorities was developed.

1) Inter-laboratory calibration of stable isotope laboratories
2) SIA analysis of a low-level consumer (e.g. barnacles) across ocean basins
3) SIA analysis of common diet taxa across ocean basins (preferably a mesopelagic and an epipelagic species)
4) SIA analysis of the stomach contents of key predator taxa (e.g. tunas)
5) comparisons of the δ¹¹N and δ¹³C of liver and white-muscle for key predator taxa (e.g. tunas)
6) comparisons of island- or seamount-caught tunas with tunas caught in the open ocean in a common geographical area
7) determine trophic-enrichment factors between a low-level consumer (e.g. a planktivore) and key predators (e.g. tunas)
8) examine correlations between the stable isotope variability and the biochemistry in ocean regions.

Figure 3. Generalized representation of the δ¹⁵N composition of particulate organic matter (POM) versus depth in the ocean. Enrichment in δ¹⁵N of sinking POM and of prey organisms imparts higher δ¹⁵N values on deep-dwelling bigeye tuna than on epipelagic yellowfin tuna. Figure from B. Graham, University of Hawaii at Manoa, Hawaii, USA.