MODELLING THE BEHAVIOUR OF TUNAS IN RELATION TO THEIR ENVIRONMENT

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by

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Addendum consisting of 1 CD-ROM, containing source code, executable programs, model results, visualisation software for PC, and curriculum vitae of the candidate

ACKNOWLEDGEMENTS

I am grateful to my supervisors, Paul Hart and David Llewellyn-Jones, for setting up the project, choosing me to do the research and for facilitating its progression through to this end. The best thing about the PhD experience is the way your mind is expanded, developed and focussed, as you try to do original research that challenges the status quo and hopefully fills some gaps and pushes back some boundaries. The worst thing is trying to find the confidence to believe in yourself at the same time as trying to please everyone else. Various people have been my mentors; various people have been my tormentors. Sometimes they have been one and the same. To all I am grateful for I have come through a stronger person and a better scientist. In this respect, thanks are due to Ed Abraham, Øyvind Fiksen, Janet Grieve, Paul Hart, Geir Huse, David Llewellyn-Jones, Alison MacDiarmid and Michael Uddstrom. I wouldn't be writing this were it not for the support I have received from my family and friends, in particular: Ed Abraham, Nicola Barnfather, Ruth Berry, Benoit Demars, Gaynor Evans, Øyvind Fiksen & Anne Berit, Mark Howard & Jo, Geir Huse & Jane, Joanna Kemp, Jan Kolaczinski, Michele Morris, Di, Hilary & Megan Oliver, Jezz Santos & Anna, Barry Shepherd, Anne Christine Utne-Palm & Håkun, and Phil Wiles.

This thesis is both my own work and the result of an unofficial team effort — it is '...an individualised assemblage of truth' (Chamberlain 1890). To avoid being accused of plagiarism I should acknowledge the following contributions: Hudson Dean calculated catch locations for the MFish tuna data; Richard Murphy and Michael Uddstrom wrote code for extracting these data into FORTRAN structures which I adapted in order to carry out the analysis presented in Chapter 2. I learned about diffusion modelling during my MSc at the University of Wales, Bangor — Ed Abraham pointed out the limits of the approach and derived a solution to the problem incorporating strain rate, which I used to investigate reaction distances by olfaction (Chapter 3). Phil Wiles helped with the coding in MATLAB. Øyvind Fiksen helped with the dynamic programming in Chapter 4; I did the maths for fish physiology and started coding the model, based on Rune Rosland's FORTRAN re-write of a basic patch selection problem from Mangel & Clark (1988), which was course material from a postgraduate seminar. Øyvind then helped with the linear interpolations in the fitness calculations, ensuring that the the model would run without sucking the memory dry. I did the simulations and wrote up the paper. A similar story applies to Chapter 5: I had the idea of combining satellite data and oceanographic model output with an individual-based model for tunas; input data were provided by Patrick Lehodey, Secretariat of the Pacific Community, New Caledonia; I then worked with Geir Huse in coding the model. Code for the artificial neural network and genetic algorithm were cut and pasted from his earlier work, code for fish physiology and sensory biology was incorporated from the optimal foraging model, and new code was developed to allow fish growth, movement, reproduction and adaptation. I acknowledge all these contributions shamelessly and with gratitude; without this collaboration my thesis would consist solely of the optimal foraging model and I might be a better programmer but a poorer scientist.

ABSTRACT

This thesis represents a quantitative synthesis of present knowledge in tuna ecology, including the development of complex behavioural and life-history models incorporating this knowledge. An underlying goal is to work towards methods that could be used with satellite data in order to predict fish locations. It is not based on field or laboratory experiment carried out by the author, but on extensive analysis of the literature documenting the work of others, analysis of data collected by scientific observers over many years, and collaborative work in the building of theoretical models. It brings together somewhat disparate disciplines in order to develop a system-level understanding of tuna ecology with the aim of developing new data analysis and fisheries management tools. The diversity of fields covered by this thesis is most apparent in Chapter 1, which gives an overview of the underlying philosophy and present level of understanding of the research. The role of modelling in science and the capabilities of different types of model are discussed. The academic sub-disciplines within which this thesis may be categorised are defined. The ecology of tunas is described as are satellite sensors that have been or could be used for fisheries applications. Case studies of such applications are reviewed. For Chapter 2, I analysed a large data set from the New Zealand surface longline fisheries for tuna, in order to identify whether and at what spatial scales tunas are aggregated. I applied methods that have not previously been used in the analysis of longline data and determined that these adult tunas are often caught in loose schools within a larger, sub-mesoscale area in which they are aggregated. In Chapter 3, I review present knowledge in tuna physiology and sensory biology, and develop and apply analytical models to determine reaction distances. This was an essential pre-cursor to the development of theoretical models in Chapters 4 & 5. The optimal foraging model had been previously anticipated in the literature but had not previously been realised. It provides a framework for addressing a long-standing and still unresolved debate as to what is 'controlling' tuna behaviour at ocean fronts. In Chapter 5, I describe and apply an important methodological synthesis for fisheries oceanography. While still requiring further development, this work nonetheless proves that it is possible to combine behavioural models for fish with whole-ocean circulation and production models that incorporate data from satellite sensors. Chapter 6 discusses further work that might follow from this thesis. Successful proposals have been made to the European Space Agency and the New Zealand Foundation for Research Science & Technology, which may now build on the work carried out here. I strongly advocate that further work to develop models linking fish distributions with environmental properties should include sea-going studies of pelagic trophic dynamics in specific areas of interest.

PREFACE

I applied to do this PhD in the summer of 1996. At that time, prospective students applied for studentships that already had a title, a rationale, and funding. The studentship for which I applied was entitled, 'Use of space data to detect oceanographic features of relevance to fisheries,' and it had funding from both the Natural Environment Research Council and VEGA Group PLC, a software development company specialising in satellite systems. The overall aim was to develop tools to guide fishing effort, based on the detection of oceanographic features from satellite-based platforms and the association of these features with species targeted in commercial fisheries.

Two very different fields are immediately apparent in the title of the studentship: satellite-based detection of oceanographic features; and determination of the relevance of such features to fish species of commercial interest. I started with a comprehensive review of the peer-reviewed scientific literature, as well as the 'grey' literature available, and it soon became obvious that research projects such as mine, though topical internationally, were at an early stage of development. Moreover, they were invariably led by scientists whose not inconsiderable expertise often lay in the field of satellite remote sensing or physical oceanography. What this has meant is that much attention has been given to methods of measuring ocean variables from satellites, with the questions to do with habitat preferences of target species being largely neglected or treated as trivial.

Meanwhile, on different research programmes and from a different perspective, fish biologists and fisheries scientists have been struggling, with varying degrees of success, to relate both the fine scale behaviour of individual fish and the large scale dynamics of fish populations, to the properties and dynamics of the ocean environment. Research to establish correlations between recruitment strength or relative abundance and oceanographic/climatic variables is the most obvious starting point, especially given the long time series of data that are often available from fisheries and oceanographic/meteorological institutes. At the other end of the spectrum of relevant spatial scales, there has been considerable research effort into fish early life history, especially quantitative estimates of larval mortality and factors affecting larval feeding success.

A common contribution that physicists make to ecology is to bring a higher level of mathematical skill to particular problems than is inherent in the discipline of biology itself. What is often missing, with some notable exceptions, is a deeper appreciation of biological science, especially with regard to cognitive and adaptive behaviour, and the evolutionary basis of ecological interactions. Whilst often oblivious to the complexities of geophysical fluid dynamics, the better and more successful research efforts in fisheries ecology have focused on a mechanistic understanding of the interactions between fish and environment. Ideally we would be able to identify simple, clear and robust relationships between variables, and for management and commercial purposes, such relationships are undoubtedly the goal. But we cannot trivialise the questions, and must work with the complexity of the natural world in order to improve our level of understanding, prior to claiming predictive ability and consequent economic benefit. We must often simplify, if only to make some kind of progress, to inch back the borders of our ignorance and have something to show for our effort. But we simplify only our methods; it is the height of human arrogance and ignorance to trivialise the very real complexity of nature.

The research chapters of the thesis could therefore have focussed on anything from atmospheric correction to animal physiology, physical oceanography to fish early life history, sensory biology to spatial statistics, all of which are relevant to the development of useful satellite based systems for fisheries management. I chose to focus on the ecological interactions underpinning the association between fish and environment. I make no overblown claims about the findings of this research. I never reached the stage of being able to provide useable forecasts for the fishing industry and I remain very sceptical of those organisations and individuals who make such claims. In the commercial world, bluffing is acceptable; in science it should not be, the commercialisation/privatisation of scientific institutions notwithstanding. What I have done is to address some of the weaker links in the arguments concerning the interactions of fish with their environment, to fill some gaps flagged in the published literature, to flag some additional gaps that may be addressed by others, and to apply some new and innovative techniques to topical problems in fisheries oceanography. This thesis is very much the product of my own thought, but I remain indebted to those who have helped me by way of stimulating discussion, constructive criticism and practical assistance. I have learned a great deal both from you and through you.

> ANARCHIST EVENING ENTERTAINMENT
> ENTRANCE NOT FOR EVERYBODY
> FOR MADMEN ONLY
> PRICE OF ADMISSION — YOUR MIND
> The Steppenwolf, Hermann Hesse

CHAPTER 1

INTRODUCTION

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1.1. MODELLING & SCIENTIFIC METHOD

Science concerns the pursuit of knowledge through reasoning, observation, analysis and evaluation, through the generation and falsification of hypotheses. The method by which it is done distinguishes the endeavour from non-science by its rigorous self-discipline, its openness and its insistence on framing 'facts' such that they are, at least in principle, testable by comparison with evidence gathered by further observation. Indeed the concept of a 'fact' does not sit easily in the vocabulary of scientists; Popper (1979) allows us only 'conjectures' that have not yet been 'refuted'. Platt (1964) gives us 'strong inference,' responding to Chamberlain's (1890) urge to use 'multiple working hypotheses,' a method that, '...distributes the effort and divides the affections', thus lessening the danger of favoured consideration for the scientist's own pet theories; '...an adequate explanation often involves the co-ordination of several causes...The true explanation [may be] necessarily complex, and the elements of the complex [may be] constantly varying' Chamberlain (1890).

It is useful to categorise models as either logical, statistical or theoretical; any of these may also become useful application tools (Loehle 1983, Fiksen 1997). Logical models are purely mathematical and are always true under the assumptions made. In themselves they are not open or subject to experimental verification, although their usefulness as application tools will depend on their ability to explain and predict observations. Statistical models are driven by data and seek to identify and perhaps describe the form of relationships that exist within the data. A statistical model cannot be true or false, but can only describe relationships well or badly. As it cannot explain *why* relationships exist, it has no explanatory power, although it may have considerable predictive power if it is able to describe relationships well, with the assumption that relationships extend past measured values. Theoretical models are not used to establish the existence of relationships, but posit mechanisms that connect variables. In this way they can be true or false, right or wrong. They can have both explanatory and predictive power. Failure to distinguish between statistical and theoretical models consitutes the 'error of pseudo-explanation' (Loehle 1987). A good statistical model will identify important

relationships, allowing one to then consider responsible mechanisms and to construct a theoretical model to explore and explain the relationships.

Models themselves can be evaluated against various criteria, depending on the type of model under consideration. Goodness of fit to data is the most obvious and the ultimate test of a model's predictive power. It is not however the only criterion by which models should be judged. A theoretical model must be able to explain the mechanism and process of the problem at hand and should first be evaluated for internal logic, elegance and explanatory power. If a consistent theory does not favourably compare with data, one must also reconsider the data and the way in which the data were acquired before rejecting the theory. Instead of talking about whether models are true or false, models are better considered as good or bad, based on both their explanatory powers and their predictive abilities. Good models may continue to be very useful, at least as conceptual tools, even if observation does not confirm their validity. And if a model has a good theoretical basis, we should not ignore it in favour of a simpler relationship simply because of lack of data, but should rather use the theory to suggest investigations that will find the data that is lacking. This is an important spin-off from adopting a theoretical approach, as the importance of the missing data may not have been appreciated before the attempt to model the process occurring.

Returning to Chamberlain (1890), there are 2 additional aspects of his essay that are relevant to this thesis, namely the concepts of 'primary study' and 'complex thought'. Primary study is distinguished from secondary, acquisitive or imitative study by requiring individual thought; 'The endeavour is to discover new truth or make a combination of truth or at least to develop by one's own effort an individualised assemblage of truth.' Of originality he writes, 'It is not necessary to this mode of study that the subject matter be new. Old material may be reworked. But it is essential that the process of thought and its results be independent and individual, not the mere following of previous lines of thought ending in predetermined results.' Complex thought, '... is contra-distinguished from the linear order of thought that is necessarily cultivated in language and mathematics because their modes are

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linear and successive. ...The mind appears to become possessed of the power of simultaneous vision from different points of view. The power of viewing phenomena analytically and synthetically appears to be gained.' In this thesis I present a series of models that investigate the physiology, behaviour and spatial dynamics of tunas in relation to their oceanic environment. The subject matter is not new, but the thesis constitutes an individualised assemblage of truth that results from an independent process of thought whereby natural phenomena have been viewed both analytically and synthetically.

1.2. ECOLOGY & FISHERIES OCEANOGRAPHY

Ecology concerns the relationships between organisms and their environment. 'Fisheries ecology' may be defined as the study of interactions between the biology of exploited fish populations and their marine or freshwater environment. Depending on the time and space scales of interest, physiological, behavioural and evolutionary ecology may be important perspectives on fish population dynamics. 'Systems ecology' is concerned with identifying mechanistic links between organisms and the environment as components of an integrated system. Within these sub-disciplines are many associated paradigms (e.g. optimal foraging theory) and methods (e.g. stochastic dynamic programming) that may be applied. 'Fisheries oceanography' is concerned with the production and dynamics of fish populations in relation to the marine environment, with emphasis on the exploration and identification of mechanisms affecting recruitment and controlling abundance. Studies in fisheries oceanography are inherently interdisciplinary, often involving meteorology, physical, chemical and biological oceanography, as well as fish biology and fisheries economics or social science. They bring together key ideas from relevant schools of thought, accepting that oceanographic variability at various spatio-temporal scales may affect spatial population dynamics, and seeking to understand how and why this occurs. The challenge in fisheries oceanography is to identify important physical characteristics of a particular environment and to consider how these relate to obligate physiological processes and life-history characteristics

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of the species of interest. Temperature effects on egg and larval survival, and on metabolic rates and stress for adults are examples of important bio-physical interactions. Water mass dynamics may be important for nutrient enrichment, concentration of food and retention of larvae and adults in favourable habitats (Bakun 1996). Different systems have different dynamics, and biological processes, even within species, may be locally adapted. Thus there is a still a need for local study of 'pure' marine biology and physics, before an understanding of the whole system may emerge.

1.3. THE ECOLOGY OF TUNAS

Tunas (family *Scombridae*, subfamily *Scombrinae*, tribe *Thunnini*) (Klawe 1977) are the most highly specialised of fishes with regard to sustained high speed swimming, and they are negatively buoyant, ram ventilators (Magnuson 1978). They are often highly migratory (Nakamura 1969) and are found in the surface waters of all the world's oceans, from 40°N to 40°S, by volume one of the largest habitats on the planet. The principal market species together constitute one of the world's largest commercial fisheries, landing over 3 million tonnes annually (Table 1.1). These fish generally have reproductive and growth rates capable of sustaining this high level of fishing mortality (but see Kearney 1991, Safina 1993 for Bluefin), in addition to high natural mortality (Murphy & Sakagawa 1977, in Brill 1996), even though they are apex predators living in a low energy environment where food is widely scattered (Blackburn 1965, Sund et al. 1981).

Table 1.1 Global catch of principal market tunas in 1994 (FAO 1997)

Species	Code	Global Catch 1994 (million tonnes)
Skipjack *Katsuwonus pelamis*	SKJ	1.5
Yellowfin *Thunnus albacares*	YFN	1.1
Bigeye *Thunnus obesus*	BIG	0.3
Albacore *Thunnus alalunga*	ALB	0.2
Northern Bluefin *Thunnus thynnus*	NBT	0.05
Southern Bluefin *Thunnus maccoyii*	SBT/STN	0.02

Tunas are thought to have a common origin as inshore tropical fishes, which through biochemical and morphological adaptations extended their ranges, becoming less dependent on environmental fluctuations and reducing competition (Sharp & Pirages 1978). The genus Thunnus is sub-divided into 2 main groups, the tropical tunas or *Neothunnus* and the temperate tunas or Bluefin group (Gibbs & Collette 1967, Collette 1978). Tropical tunas are more closely associated with warmer latitudes and, with the exception of Bigeye, shallower depths; their ranges are limited vertically by the base of the thermocline, and horizontally by frontal boundaries with colder waters (Nakamura 1969, Sund et al. 1981, Block et al. 1997). Temperate tunas have higher latitudinal ranges and forage in deeper waters (Sund et al. 1981, Holland et al. 1990, 1992, Dewar et al. 1994) reflecting their adaptation to colder waters.

Tunas have the ability to maintain muscle temperature above ambient water temperature, which is the result of heat exchange in the countercurrent rete of the vascular system to the trunk musculature (Kishinouye 1923, Carey & Lawson 1973, Sharp & Vlymen 1978, Stevens & Neill, 1978). A recent paper argues that 'Coevolutionary changes in red muscle distribution and quantity and in vascular specializations for heat conservation have lead to different macroevolutionary trajectories among the now 5 genera and 14 species of tunas and appear to reflect the influence of changing paleoecological and paleoceanographic conditions, including cooling, that occurred in the Tertiary' (Graham & Dickson 2000). Tunas are also capable of controlling heat production and dissipation, in addition to both passive and behavioural thermoregulation (Dizon & Brill 1979, Holland et al. 1992, Dewar et al. 1994). There may be several advantages to tunas of warm body temperatures and large thermal inertia. Foraging range may be increased in both horizontal and vertical dimensions, by the ability to maintain body temperature (Neill et al. 1976, Graham & Deiner 1978). This facility may also be useful when escaping from predators. High muscle temperature may also result in greater power availability from a given muscle mass, due to more efficient chemical to mechanical energy conversion, thus enabling higher maximum swimming speeds (Carey et al.

1971, Bone 1978, Carey 1982, Altringham & Block 1996). Elevated body temperatures have been related to increased swimming speed, although the direction of the cause and effect relationship was unclear (Brill 1978). Recent reviews (Brill 1994a, 1996) suggest that the high performance physiology of tunas, of which elevated body temperature is a result, has evolved to permit rapid somatic and gonadal growth, rapid digestion, and rapid recovery from exhaustive exercise, abilities which are all central to success in the pelagic environment.

Tunas are predominantly visual predators (Nakamura 1967, Kawamura et al. 1981), feeding opportunistically and unselectively on micro-nekton, including epipelagic fish, molluscs and crustaceans, and the larvae of these groups (Blackburn 1968). Albacore are thought not to feed actively at night (Iverson 1962) although they will take prey if it is encountered, as evidenced by occasional catches using lures. Yellowfin have been observed to swim closer to the surface at night (Holland et al. 1990), which was attributed to searching, using available moonlight, for squid and shrimp that come up from greater daytime depths. The role of water clarity in determining visual feeding efficiency may also be important for tunas (Murphy 1959), highlighting the need to distinguish between prey abundance and prey availability when characterising habitats and seeking to understand behaviour (Marr 1951).

The foraging behaviour of tunas includes vertical excursions within the surface waters, into and below the thermocline, and horizontal excursions within the same water mass or into and across frontal boundaries between water masses (Holland et al. 1990, Block et al. 1997, Brill et al. 1999). The extent of these movements outside the warm surface waters is limited by the acute reductions in water temperature that are experienced. Despite the mechanisms of heat conservation available to tunas, temperature limitation of foraging range is suggested by laboratory experiment (Dizon et al. 1977, Barkley et al. 1978, Brill et al. 1998) and apparent in field observations (Blackburn 1965, Sund et al. 1981, Brill 1994a, Brill et al. 1999).

1.3.1. Tropical tunas

Skipjack *Katsuwonus pelamis* **(Linnaeus, 1758).** Skipjack (Fig. 1.1) are cosmopolitan in tropical and warm-temperate waters (15°C to 30°C; 58°S to 47°N) although they are not found in the eastern Mediterranean Sea and the Black Sea. The species is highly vagile, but not necessarily highly migratory (Kearney 1991). These fish are found in offshore waters, and their larvae are restricted to waters with surface temperatures of at least 25°C. Skipjack exhibit a strong tendency to school in surface waters, and are often found associated with birds, drifting objects, sharks and whales. They feed on fishes, crustaceans, cephalopods and molluscs, and cannibalism is common. In turn they are preyed upon by large pelagic fishes. They are usually fished by purse seine or by trolling.

Yellowfin *Thunnus albacares* **(Bonnaterre, 1788).** Yellowfin (Fig. 1.2) have a worldwide distribution in tropical and subtropical seas (15°C to 31°C; 45°S to 45°N) but are absent from the Mediterranean. They are a highly migratory oceanic species. They school primarily by size, often in association with floating objects, and larger fish frequently school with porpoises. They are sensitive to low concentrations of oxygen and so are often limited to depths <200 m. Peak spawning occurs in batches during summer.

Bigeye *Thunnus obesus* **(Lowe, 1839).** Bigeye (Fig. 1.3) are found in tropical and subtropical waters of the Atlantic, Indian and Pacific oceans. Preferred surface water temperatures are from 13°C to 29°C, and are optimal between 17°C and 22°C. Variation in occurrence is closely related to seasonal and climatic changes in SST and thermocline depth. Juveniles and small adults school at the surface in mono-specific groups or with other tunas, and may be associated with floating objects. Adults occupy deeper waters but may also come to the surface. Bigeye are considered to be highly migratory and vulnerable to over-exploitation.

Fig. 1.1 Skipjack *Katsuwonus pelamis*
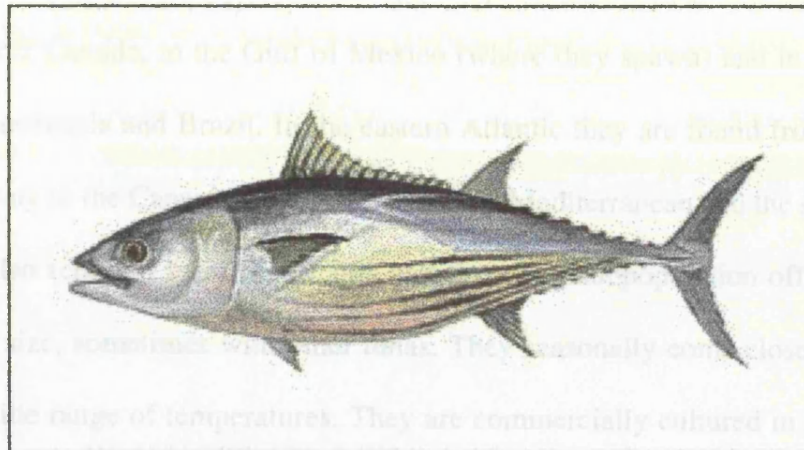max. size: 110 cm; max. weight: 35 kg

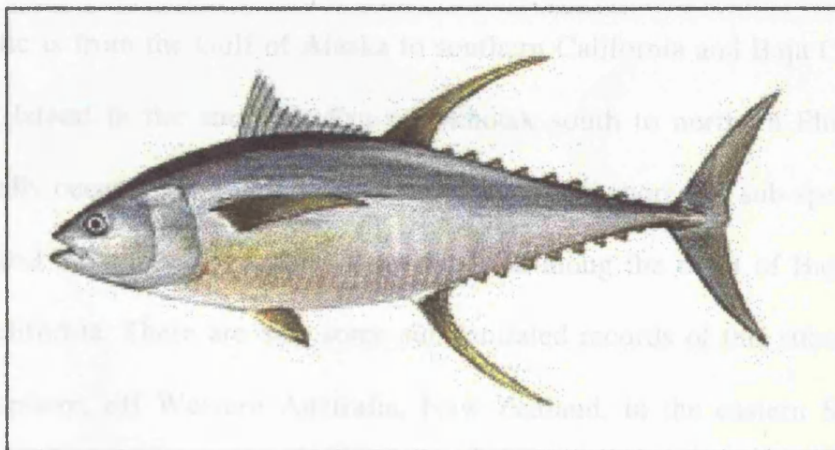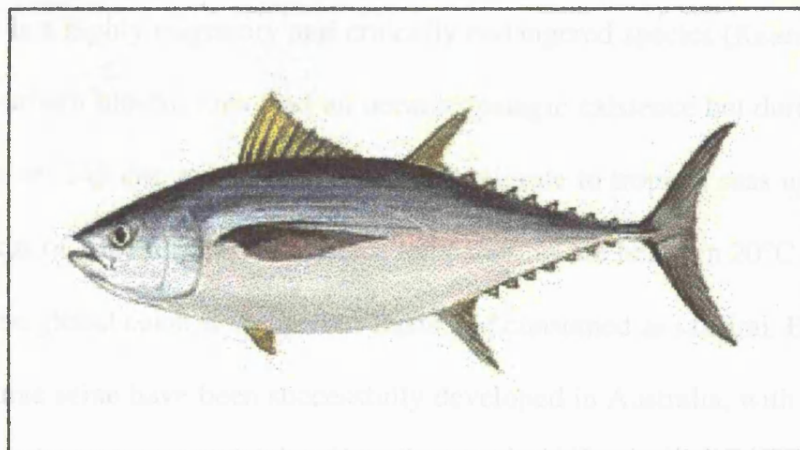Fig. 1.2 Yellowfin *Katsuwonus pelamis*
max. size: 280 cm; max.weight: 200 kg

Fig. 1.3 Bigeye *Thunnus obesus*
max. size: 250 cm; max. weight: 210 kg

1.3.2. Temperate tunas

Northern bluefin tuna *Thunnus thynnus* (Linnaeus, 1758). Bluefin (Fig. 1.4) are highly migratory oceanic fish with a subtropical distribution (70°S to 40°N). In the western Atlantic they are found off Canada, in the Gulf of Mexico (where they spawn) and in the Caribbean Sea, down to Venezuela and Brazil. In the eastern Atlantic they are found from the Lofoten Islands off Norway to the Canary Islands, including the Mediterranean and the southern Black Sea. They are also reported from Mauritania and there is a subpopulation off South Africa. They school by size, sometimes with other tunas. They seasonally come closer to shore and can tolerate a wide range of temperatures. They are commercially cultured in Japan, and are utilised fresh for sashimi (but are also canned). Northern Bluefin in the Pacific is recognised as a sub-species, *Thunnus thynnus orientalis* Temminck & Schlegel (1844). Distribution in the North Pacific is from the Gulf of Alaska to southern California and Baja California and from Sakhalin Island in the southern Sea of Okhotsk south to northern Philippines. An epipelagic, usually oceanic fish that seasonally comes close to shore, the sub-species migrates between June and September in a northward direction along the coast of Baja California, Mexico and California. There are also some substantiated records of this subspecies in the southern hemisphere, off Western Australia, New Zealand, in the eastern South Pacific (37°11'S, 114°41'W) and Gulf of Papua.

A single stock of Southern Bluefin tuna *Thunnus maccoyii* Castelnau (1872) inhabits the temperate and cold seas of the southern hemisphere, mainly between 30°S and 50°S, but to nearly 60°S. It is a highly migratory and critically endangered species (Kearney 1991). By maturity, most southern bluefin tuna lead an oceanic, pelagic existence but during spawning, large fish (max. size: 245 cm; max. weight: 260 kg) migrate to tropical seas up to 10°S, off the north-west coast of Australia, where surface temperatures are between 20°C and 30°C. As much as 98% of the global catch is shipped to Japan and consumed as sashimi. Efforts to farm SBT caught by purse seine have been successfully developed in Australia, with production at 4700 tonnes in 1998.

Albacore *Thunnus alalunga* (Bonnaterre, 1788). Albacore (Fig. 1.5) are cosmopolitan in the tropical and temperate waters (45°S to 50°N) of all oceans, including the Mediterranean Sea, but are not found at the surface between 10°N and 10°S. A highly migratory epi- and mesopelagic species, they are abundant in surface waters of 15.6°C to 19.4°C; deeper swimming, large albacore are found in waters of 13.5°C to 25.2°C, although temperatures as low as 9.5°C may be tolerated for short periods. They form mixed schools, which may be associated with floating objects, including sargassum weeds. Albacore meat is not of sashimi quality but forms the basis of commercial fisheries for canned tuna.

Fig. 1.4 Northern bluefin tuna *Thunnus thynnus*
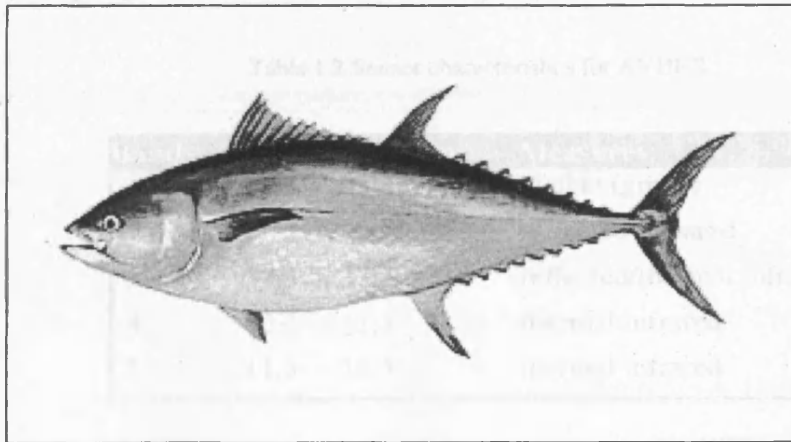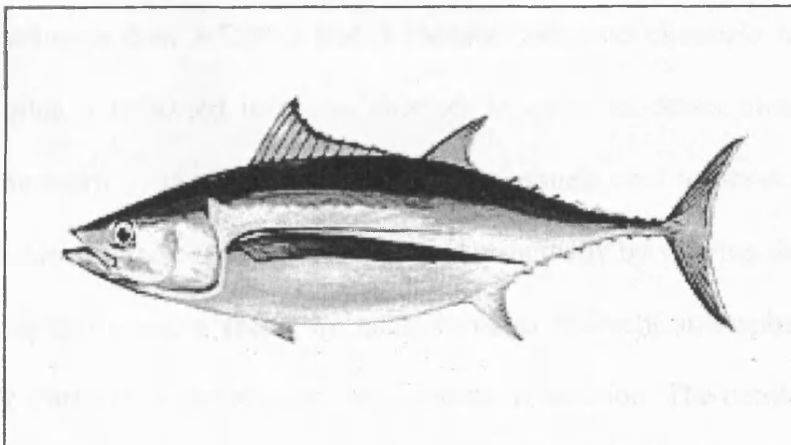max. size: 458.0 cm; max.weight: 684 kg

Fig. 1.5 Albacore *Thunnus alalunga*
max. size: 130cm; max. weight: 45kg

Tuna illustrations from Raver (1984)

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1.4. SATELLITE REMOTE SENSING & FISHERIES

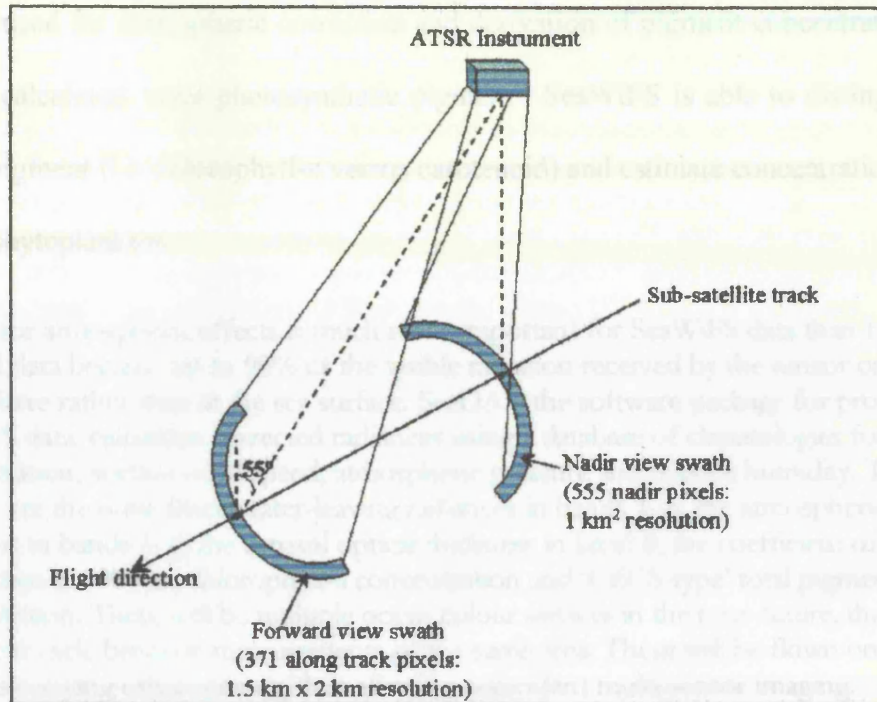## 1.4.1. Visible and infra-red radiometers

Advanced Very High Resolution Radiometer (AVHRR). The AVHRR is a scanning radiometer with 5 detectors in the visible and infra-red wavelengths. The 3 channels in the infra-red band detect heat radiation from the sea surface. On account of the intervening atmosphere, the sea surface appears cooler from above by several degrees, for which a very accurate correction must be made; sea surface temperature may then be calculated. AVHRRs have been flown on NOAA satellites since the mid-1970s. These polar-orbiting satellites always operate as a pair, passing close to both poles in an almost north-south orbit, ensuring that data for any region of the Earth are no more than 6 h old.

Table 1.2 Sensor characteristics for AVHRR

Band	Wavelength (μm)	Measures:
1	0.58 - 0.68	visible (green)
2	0.725 - 1.00	reflected infrared
3	3.55 - 3.93	reflected/thermal infrared
4	10.3 - 11.3	thermal infrared
5	11.5 - 12.5	thermal infrared

Along Track Scanning Radiometer (ATSR). The ATSR is an advanced imaging radiometer flown on the European Space Agency satellites, ERS 1 & 2. The main objective for ATSR was to measure global SST with the high levels of accuracy required for climate research. In order to achieve this, ATSR-1 had 3 thermal infra-red channels matching those of the AVHRR plus a reflected infra-red channel in order to detect clouds by day. ATSR-2, launched in April 1995 on ERS 2, has 3 extra channels used to develop applications of data over land. Atmospheric correction is achieved principally by viewing the Earth at 2 angles. As the 2 views of the same scene are taken through different atmospheric path lengths, it is possible to correct for the effect of atmospheric absorption. The combination of radiometric sensitivity, stability and the dual-angle viewing geometry enables SST to be measured to an accuracy of 0.2–0.3°K. There will be an 'advanced ATSR' (AATSR) on ENVISAT-1.

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Fig. 1.6 Viewing Geometry for ATSR & AATSR

ATSR Instrument

Sub-satellite track

Nadir view swath
(555 nadir pixels:
1 km² resolution)

55°

Flight direction

Forward view swath
(371 along track pixels:
1.5 km x 2 km resolution)

The Sea-viewing Wide Field-of-view Sensor (SeaWiFS). SeaWiFS has 8 bands in the visible and near-infrared wavelengths (Table 1.3) and is designed to measure ocean colour, a physical property largely determined by biological (photosynthetic) processes. The sensor is a successor to the Coastal Zone Colour Scanner (CZCS), which operated from 1978 to 1986. The CZCS was a 'proof-of-concept' mission, which established the feasibility of global monitoring of bio-optical variability, data that is critical for the study of oceanic primary production and global biogeochemistry.

Table 1.3 Sensor characteristics for SeaWiFS

Wave length [μm]	Colour:	Used to measure:
0.402-0.422	Violet	Dissolved organics
0.433-0.453	Blue	Chlorophyll
0.480-0.500	Blue/green	Chlorophyll / k490
0.500-0.520	Green	Chlorophyll
0.545-0.565	Green/yellow	Chlorophyll
0.660-0.680	Red	Aerosols
0.745-0.785	Near infrared	Aerosols
0.845-0.885	Near infrared	Aerosols

SeaWiFS contains specific enhancements both in terms of its engineering capabilities and in the algorithms used for atmospheric correction and derivation of pigment concentrations. Whereas the CZCS calculated 'total photosynthetic pigment', SeaWiFS is able to distinguish different classes of pigment (i.e. chlorophyll-a versus carotenoid) and estimate concentrations of different classes of phytoplankton.

Correction for atmospheric effects is much more important for SeaWiFS data than for AVHRR infrared data because up to 90% of the visible radiation received by the sensor originates in the atmosphere rather than at the sea surface. SeaDAS, the software package for processing SeaWiFS data, calculates corrected radiances using a database of climatologies for ozone concentration, surface wind speed, atmospheric pressure and relative humidity. The main outputs are the normalised water-leaving radiances in bands 1–5, the atmospheric aerosol radiances in bands 6–8, the aerosol optical thickness in band 8, the coefficient of diffuse attenuation at 490 nm, chlorophyll-a concentration and 'CZCS-type' total pigment concentration. There will be multiple ocean colour sensors in the near-future, thus minimising the repeat cycle between measurements of the same area. These will be flown on board satellites carrying other sensors, thus allowing coincident multi-sensor imaging.
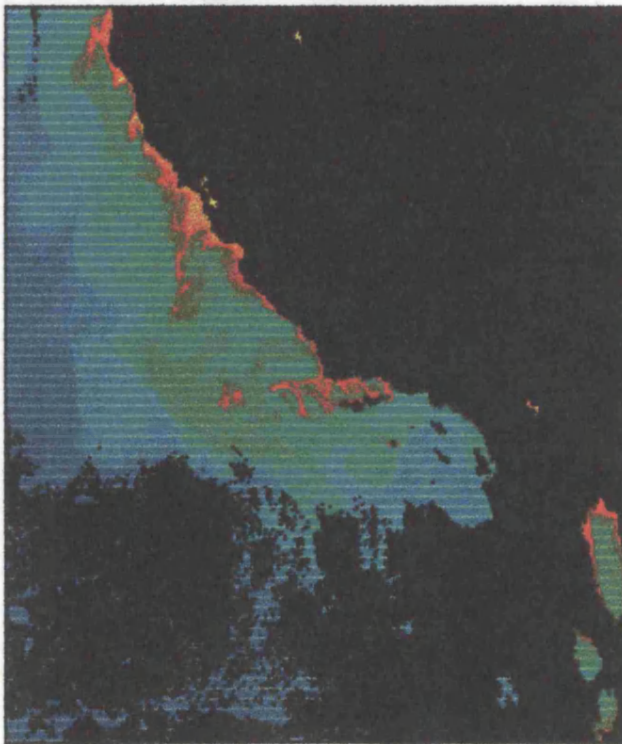
Fig. 1.7 SeaWiFS Image of Diffusion Attenuation Coefficient (k_{490}) off the West Coast of the USA. Land and cloud are masked white. Coastal upwelling filaments (turbid waters, orange/red) and ocean fronts (transition from red to green, turbid to clear water) are clearly visible — albacore aggregate at these fronts (Laurs et al. 1984). k_{490} is an important parameter affecting the visual range and therefore hunting efficiency of tunas (Kirby et al. 2000, Chapter 4). k_{490} is higher in the plankton-rich coastal waters, which are also colder and may be rich in food.

1.4.2. Passive microwave radiometers

Measurement of SST by satellite microwave radiometers has been an elusive goal for many years. The important feature of microwave retrievals is that SST can be measured through clouds, a distinct advantage over infrared SST observations that require a cloud-free field of view. Microwave retrievals are unaffected by aerosols and insensitive to atmospheric water vapour, although they are sensitive to sea-surface roughness. Early radiometers were poorly calibrated and later radiometers lacked the low frequency channels needed to retrieve SST. At present there are passive microwave sensors capable of measuring SST, although their use by ocean scientists is not widespread, and ocean areas with persistent cloud coverage can now be viewed on a daily basis. The Special Sensor Microwave /Imager (SSM/I) is a 7 channel, 4 frequency system carried on Defense Meteorological Satellite Program (DMSP) satellites, measuring atmospheric, ocean and terrain microwave brightness temperatures. These data are used to derive: SST, land surface temperature, ocean surface wind speed, areal cover by ice, age of ice, ice edge, precipitation, cloud liquid water, integrated water vapour, soil moisture and snow cover. In 1997, a well-calibrated radiometer with a 10.7 GHz channel was launched aboard the Tropical Rainfall Measuring Mission (TRMM) satellite, a joint program between NASA and NASDA. A primary function of the TRMM Microwave Imager (TMI) SST retrieval algorithm is the removal of surface roughness effects. A further passive microwave sensor (AMSR) will be launched on ADEOS 2.
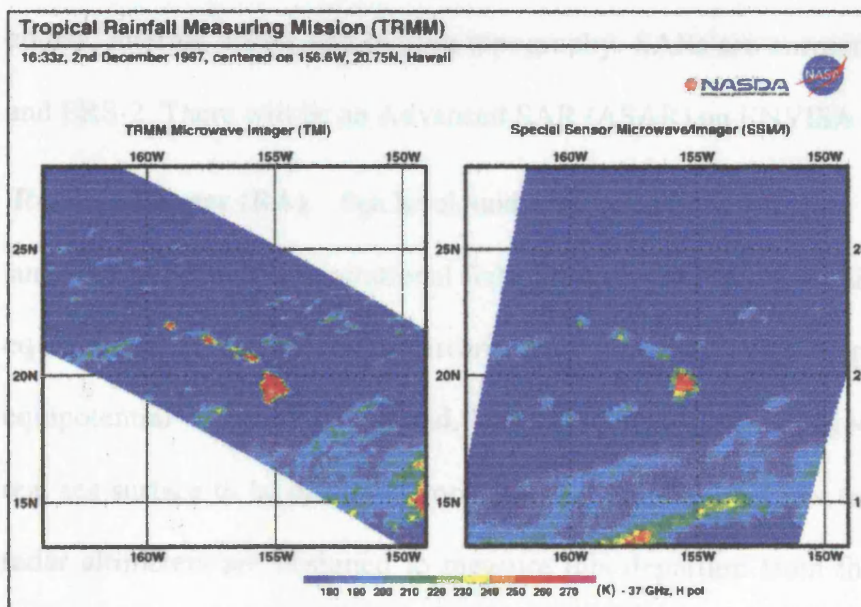

Fig. 1.8 Simultaneous images from TMI & SSMI. Note finer spatial resolution of TMI

1.4.3. Active microwave radiometers

Synthetic Aperture Radar (SAR). SAR provides the spatial pattern of reflected microwave energy from an elliptical area or 'footprint' on the Earth's surface and imagery is built up from the time delay and strength of the returned signals. It is thought that resonance between the radar and surface capillary waves is the primary mechanism for backscattering radar pulses. Capillary waves have wavelengths of less than 10 cm, and form in response to wind stress.

The SAR directly images the spatial distribution of the Bragg-scale capillary waves, referred to as sea surface roughness. This may be affected by longer gravity waves and other oceanographic and atmospheric features, such as: variable wind speed, changes in stratification in the atmospheric boundary layer, and variable currents associated with fronts, eddies, internal waves and bottom topography. SARs are currently carried on RADARSAT and ERS-2. There will be an Advanced SAR (ASAR) on ENVISAT.

Radar altimeter (RA). Sea level, undisturbed by waves or tides etc., is an equipotential surface of the Earth's gravitational field. Density differences within the solid earth distort the equipotential, leading to departures from the standard ellipsoid. The real resulting equipotential surface is the Geoid. The permanent, time-averaged ocean currents cause the real sea surface to be different from the marine geoid by a few tens of centimetres. Satellite radar altimeters are designed to measure this departure from the geoid by measuring the distance between the satellite and the nadir point to within a precision of a few centimetres. A short pulse of microwaves is transmitted vertically downwards, which illuminates a footprint on the sea surface of 2–12 km in width, depending on sea state. The echoes from these transmissions are received and the distance covered by the pulse is calculated using the time delay. Corrections are applied to account for refraction by the atmosphere and for the effect of sea state. Sea surface height measurements may be used to monitor the permanent ocean circulation and the large scale temporal variations that may be exhibited. Mesoscale current systems may also be studied, and the RA is particularly useful for measuring the dynamic

topography associated with meandering, vortex shedding and the migration of eddies. The geostrophic currents associated with these features may then be calculated from the sea surface slope. In addition to measuring sea level anomaly, RAs may also be used to deduce wave height, by measuring the slope of the return pulse, and to calculate wind speed, from the fraction of power returned to the sensor. RAs are presently flown on ERS-2, TOPEX/POSEIDON, and the GFO satellites and there will be an RA on ENVISAT I.

The Gulf of Tehuantepec, Mexico, is an important area for yellowfin tuna fisheries. Blackburn (1962, 1963) has described how tuna abundance increases ~3 mo after upwelling events; this lag is attributed to the time required for the development of micronektonic food for the tunas.

The AVHRR image above (Fig. 1.9) shows the response of the Gulf of Tehuantepec, Mexico to a cold, northerly wind burst. An anti-cyclonic eddy is formed in the western Gulf and the central Gulf waters are cooled by mixing and upwelling. The SAR frames left (Fig. 1.10) show the warm-core eddy 2 days later, with high radar backscatter (bright) and the colder mixed waters (dark). Circles illustrate concentric bands of current shear. Lines point to a baroclinic instability at the eddy boundary. The area of the SAR frames is outlined on the AVHRR image. From Kirby et al. (1997).
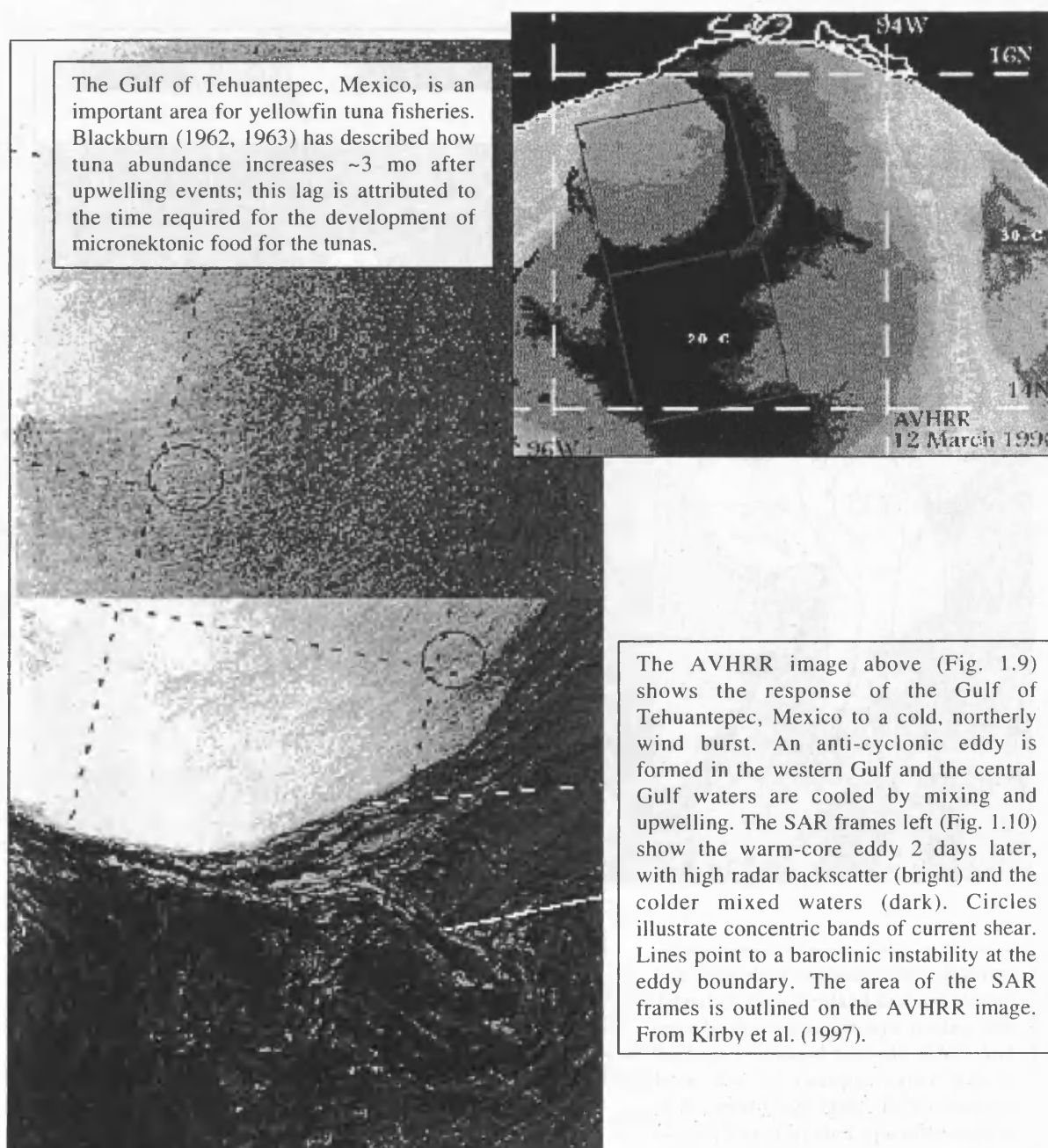
Fig. 1.11 Sea-surface temperature and current anomaly composites for 26 July to 5 August 1996. Temperatures are a 10 d composite matching the 10 d Topex-Poseidon cycle from which the current patterns are deduced. These currents are indicated by streamlines. Their strength is measured by the gridded small arrows: the longer the arrows the stronger the current. SST data are from the NIWA SST Archive (Uddstrom & Oien 1999) extracted and co-located with SSH by Andrew Laing, NIWA

26 July to 5 August 1996 (UTC)
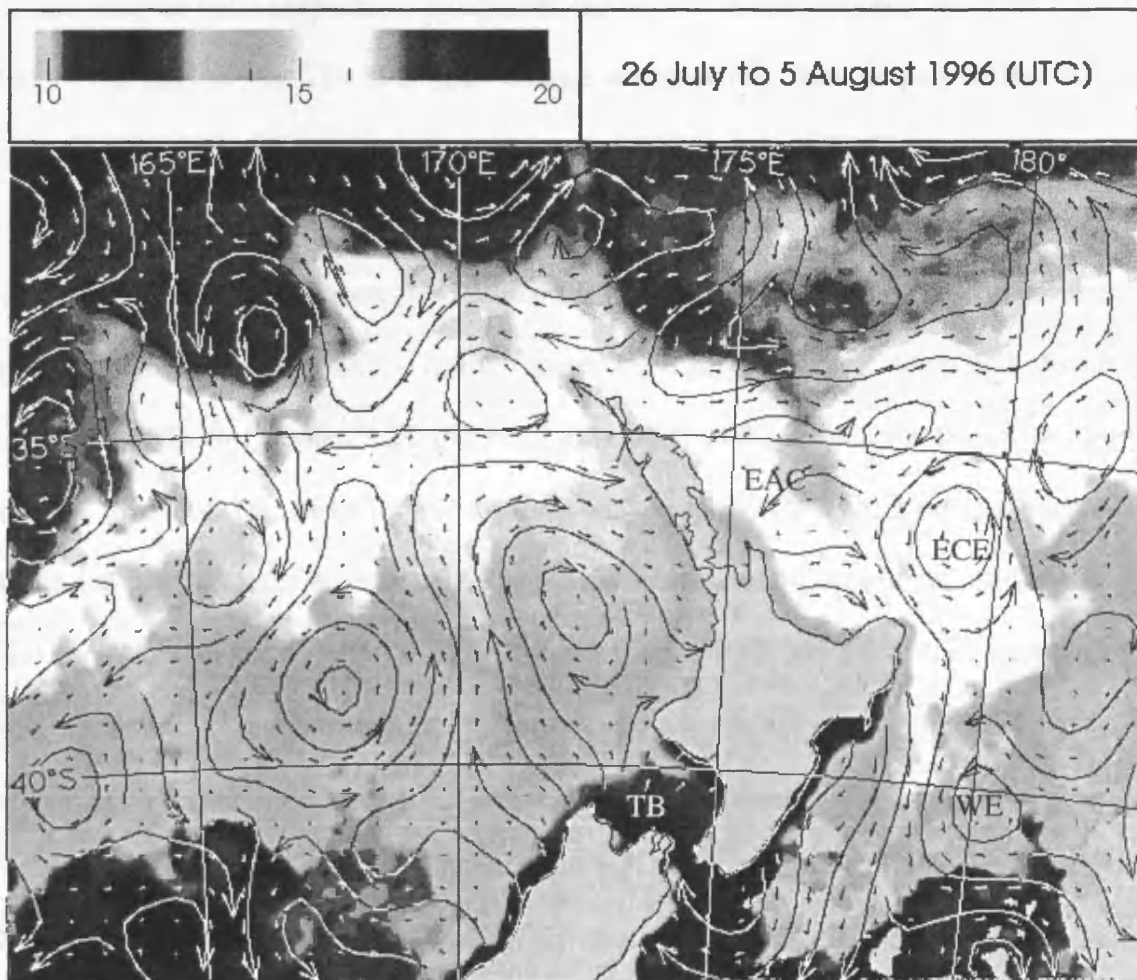
This image captures important oceanographic features around the North Island of New Zealand that are related to fisheries for tunas to the north (Bigeye occupy the warm waters of the East Auckland Current, EAC) and north-east (Southern Bluefin occupy cooler waters around the edge of the East Cape Eddy, ECE), and for squid to the south-west (found in cool upwelled waters in the Taranaki Bight, TB). In addition, the Wairapa Eddy (WE) off the east coast is thought to retain larvae, supporting coastal populations of rock lobster *Jasus edwardsiii* (Chiswell & Booth 1999)

Radar Scatterometers. Winds over the ocean modulate air-sea changes in heat, moisture, gases and particulates, regulating the crucial bond between atmosphere and ocean that establishes and maintains global and regional weather and climate. In the past, weather data could be easily acquired over land but knowledge of surface winds over oceans had to come from ships and buoys. 'Radar scatterometers' have their origin in early radar used in World War II. Measurements over oceans were corrupted by noise and it was not known at that time that this was the radar response to winds over the oceans. Radar response was first related to wind in the late 1960s. The first spacebourne scatterometer flew as part of the 'Skylab' missions in the early 1970s. The Seasat-A Satellite Scatterometer (SASS) operated from June to October 1978 and proved that accurate wind velocity measurements could be made from space. A single-swath scatterometer flew on ERS-1 and the first dual-swath scatterometer to fly since Seasat was the NASA Scatterometer (NSCAT) on board ADEOS-1. Since the demise of ADEOS-1, QuikSCAT has been developed and launched by NASA as a quick recovery mission. The SeaWinds instrument on the QuikSCAT satellite is a specialised microwave radar that measures near-surface wind speed and direction under all weather and cloud conditions over the Earth's oceans. It uses a rotating dish antenna with 2 spot beams that sweep in a circular pattern, radiating microwave pulses at a frequency of 13.4 GHz. The instrument collects data over ocean, land and ice in a continuous 1800 km swath, covering 90% of the Earth's surface each day. A SeaWinds scatterometer will also be launched on ADEOS II. Scatterometers are not yet widely used for fisheries research. However, the fact that much coastal upwelling is wind-driven, either directly or indirectly, and wind-generated turbulence, proportional to wind speed cubed (w^3), has significant influence on larval fish feeding success (Fiksen et al. 1998) survival and recruitment (Cury & Roy 1989) may mean that more attention is given to these data in the future. The 'Pelagic Fisheries Research Program' in Hawaii is studying the effect of oceanographic variability on bigeye tuna catch-per-unit-effort (CPUE), and will consider satellite scatterometer data along with other relevant variables (J. Polovina pers. comm, URL: www.soeast.hawaii.edu/PFRP).
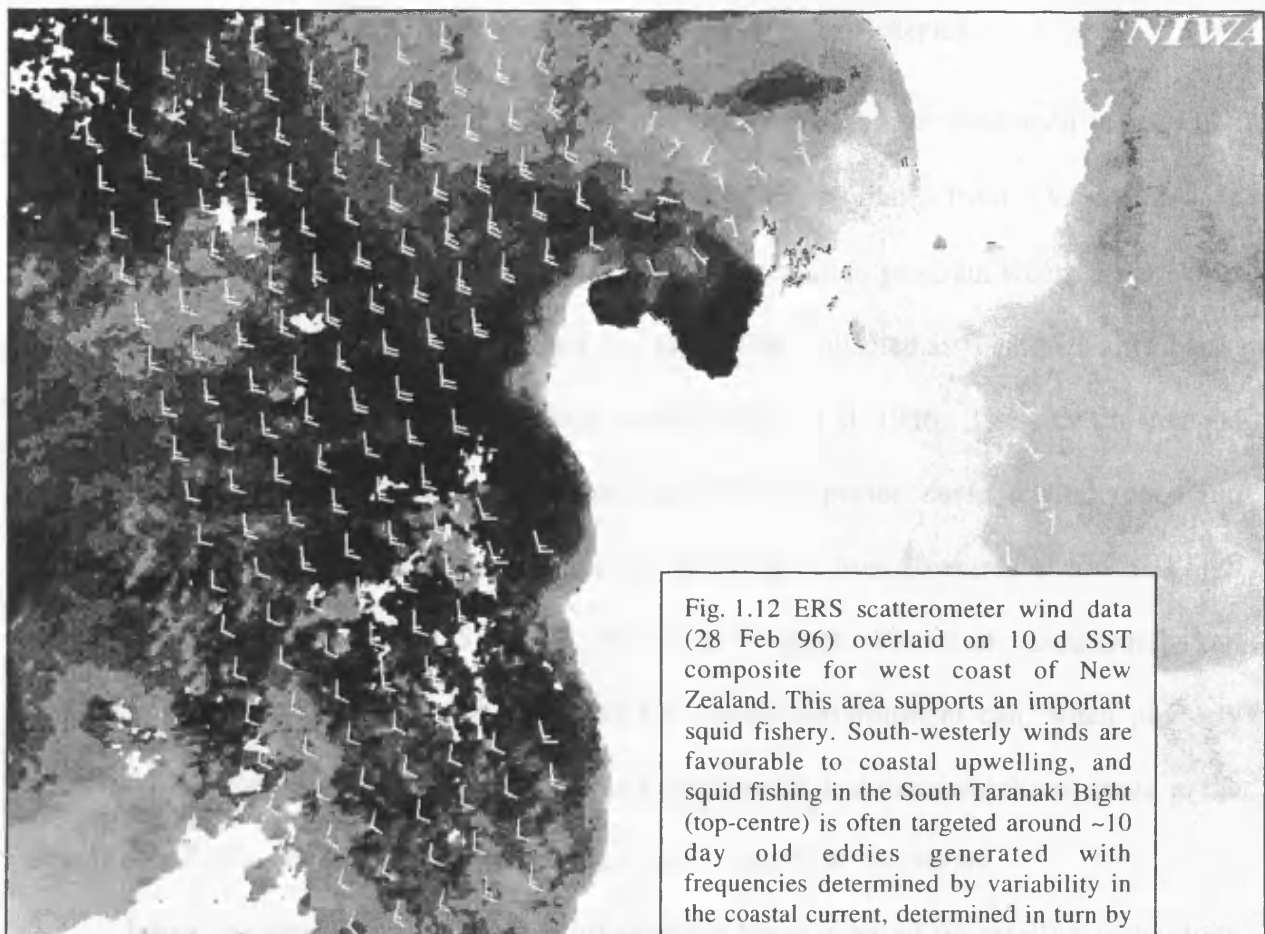
Fig. 1.12 ERS scatterometer wind data (28 Feb 96) overlaid on 10 d SST composite for west coast of New Zealand. This area supports an important squid fishery. South-westerly winds are favourable to coastal upwelling, and squid fishing in the South Taranaki Bight (top-centre) is often targeted around ~10 day old eddies generated with frequencies determined by variability in the coastal current, determined in turn by local wind forcing and the spring-neaps tidal cycle (Bowman et al. 1983) (black, SST > 20°C; white, cloud/land/SST < 15°C). SST data are from NIWA SST archive (Uddstrom & Oien 1999) extracted and collocated with scatterometer data by Andrew Laing

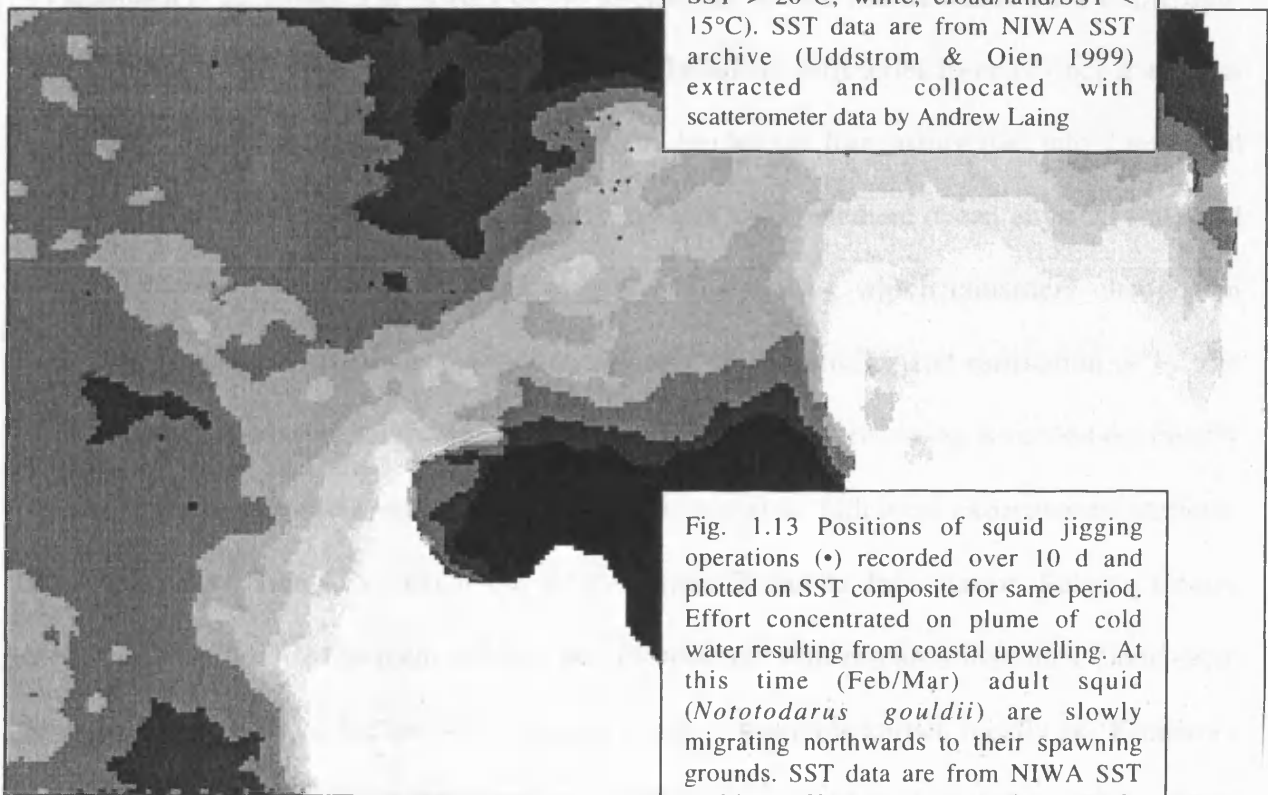Fig. 1.13 Positions of squid jigging operations (•) recorded over 10 d and plotted on SST composite for same period. Effort concentrated on plume of cold water resulting from coastal upwelling. At this time (Feb/Mar) adult squid (*Nototodarus gouldii*) are slowly migrating northwards to their spawning grounds. SST data are from NIWA SST archive (Uddstrom & Oien 1999) extracted and collocated with fisheries data by David S. Kirby

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1.4.4. Case studies in remote sensing for fisheries

Satellite sea surface temperature (SST) data have been available to fishermen in the USA since the mid-1970s and maps of thermal fronts have been produced from AVHRR data. In 1981 NASA and NOAA initiated a 2 yr fisheries demonstration program where a variety of remotely sensed and numerically simulated data types were collected as 'Fisheries-aid Charts' and faxed or radioed to participating vessels (Montgomery et al. 1986). These charts mapped and gave a 5 d forecast for critical SST for selected fish species, surface wind speed and direction, combined wave heights and direction, location of fronts, centres of low and high atmospheric pressure, coastal SST and mixed layer depth. The study concluded that, '...conventional and satellite derived data of the marine environment can, when properly combined and correlated, offer the commercial fisherman tactical tools which can result in the selection of fishing strategies for more efficient and economical operations.'

Japan has developed a Fisheries Information Service based on satellite technology (Yamanaka et al. 1988). The history of the forecasting service can be traced back to the mid-1930's when the Japan Broadcasting Corporation broadcast a fisheries forecast once a week as part of the news report. The present day system divides the forecasting role into 2 temporal perspectives: short-term forecasting, which considers the immediate ocean physical state and likely effects on fish locations, and long-term forecasting which considers changes in catchability and total fisheries production through the monitoring and estimation of factors such as spawning, larval survival and recruitment. Long-term forecasting is carried out chiefly by the national fisheries research institutes in collaboration with local experimental stations. Short-term forecasting is carried out by the Japan Fisheries Information Service Centre (JAFIC), a central Government agency, in collaboration with research institutes. Short-term forecasting is based on the location of ocean fronts, a principle known locally as 'Kitahara's Law' (after Kitahara 1922, in Yamanaka et al. 1988) which supported the fishermen's premise that fish gather where 2 different seas converge. Where the warm Kurishio Current from the South Pacific meets the cold Oyashio current from the Kuril Islands, a fishery is supported

that produces 15% of world fish products (Tameishi *et al.*, 1993). The predictive system which assists the exploitation of this fishery is based principally around preferred temperatures and temperature gradients for given fish species. Once the analysis has been carried out, maps of fishing potential are then transmitted to vessels and other subscribers, including research institutes and fishing administrations. The system was applied to SST data from the NOAA satellites and tested against skipjack tuna catch data. For the years 1982–85, fishing potential F was positive in 82% of productive fishing grounds and was negative for 94% of unproductive areas. The system may have been developed further since this time but details have not been published.

The tuna, swordfish and sardine fisheries off continental Portugal and the Azores are supported operationally by the University of Lisbon Oceanography Group (Santos & Fiúza 1992). The operational support consists of the provision of SST charts based on satellite (AVHRR) observations and the annotation of these charts to include gradient analysis for the location of thermal fronts. The group is also investigating the relationships between fish aggregations and the distributions of oceanographic variables. There is evidence that swordfish concentrate in warm, clear water at intermediate distances from the strong thermal front separating upwelled waters from the open ocean during periods of relaxation in coastal upwelling. Inter-annual variability in swordfish catch is inversely correlated with the strength of coastal upwelling. The reverse is true for bigeye and albacore tuna, which aggregate just seaward of upwelling filaments. The tunas are assumed to aggregate at the fronts in order to feed, as there is evidence that sardines are found in, 'moderately cool, relatively old upwelling waters' on the inside of thermal fronts (Santos & Fiúza 1992).

There has been considerable research into the physical and biological variability of the Upwelling Zone off the coast of North West Africa. There is year-round Ekman upwelling in the major part of this zone with seasonal upwelling to the South dependent on the extent of the northerly winds. This upwelling supports significant fishing grounds for tuna and for many other species of fish, cephalopods and crustacea. Until the 1960s the Spanish fleet was

the only foreign fleet in the area but since that time it has been joined by other European and oriental fleets from over 25 countries (Clementé-Colón et al. 1992).

This is certainly a promising area for the application of remote sensing for operational fisheries forecasting. International fleets already direct their effort towards waters that have been advected downstream of their point of origin at the surface, and satellite sensors of both SST and ocean colour could provide useful tools for tracking these waters (Clementé-Colón et al. 1992). The highest Catch per unit effort (CPUE) for skipjack tuna is recorded at upwelling fronts (Ramos et al. 1992). In the Canary Isles, the persistent eddies associated with the island wake behind Gran Canaria can constitute a thermal boundary for further northward movement of skipjack. The fishing ground is compressed by the cold core eddy towards the warmer island wake. As the SST is homogenised, the surface wake extinction determines the spreading of fishing locations around the island (Ramos et al. 1991).

Scientists from the French 'Scientific Research Institute for Development and Co-operation' (ORSTOM), supporting French fleets from the South Pacific to the North Atlantic, have developed a variety of forecasting aids with which to assist and direct fishing effort. (Clementé-Colón et al. 1992). In the Eastern Tropical Atlantic, a model called 'PREVI-PECHE' is used (Stretta 1991). The fishing potential of an area is calculated by comparing the evolution of temperature distribution with an 'ideal thermal scenario'. Sea surface temperature on the day of catch is not thought to be the sole determinant of tuna distribution; instead the evolution of a water mass over time is considered, with regard to whether it is likely to support concentrations of tuna forage. The delay between the onset of upwelling and the presence of tuna forage has been estimated as ~4–6 wk (Mendelsshon & Roy 1986). A high concentration of tuna could therefore be expected in an area where a decrease in SST at the start of the enrichment process is followed by a regular increase in temperature over this time period.

Longer term forecasting requires relationships between ocean variables and fish life history characteristics to be identified at larger spatio-temporal scales. Apparent shifts in the distribution of Pacific skipjack tuna may be linked to large zonal displacements of the convergence zone marking the boundary of the western Pacific warm pool (Lehodey et al. 1997). These displacements occur during ENSO events and so it should be possible to predict, months in advance, the region of highest skipjack abundance. For the South Atlantic squid (*Illex argentinus*) links between recruitment variability and the environment have recently been examined (Waluda et al. 1999). Correlation analyses show that when temperatures are colder in the spawning grounds of the northern Patagonian shelf during the period of hatching, better catches arise in the fishery in the following season. No significant correlation was obtained between squid catches and SST co-incident with the period of the fishery. Further analysis showed that cross-correlation exists between SST anomalies in the western Pacific and in the spawning grounds of the northern Patagonian shelf after a lag of 4.5 to 5 yr. Therefore, not only can year class strength be predicted 8 mo in advance from SSTs observed in the spawning grounds, but planning may be enabled some 6 yr in advance based on these longer spatio-temporal correlations.

By using altimeter data to compute geostrophic surface currents, larval transport dynamics can be investigated (Polovina 1999, Chiswell & Booth 1999). By seeding the circulation with a passive tracer representing the larvae, Chiswell & Booth (1999) are able to conclude that an anticyclonic eddy is responsible for larval retention which may in turn be responsible for maintaining a population of rock lobster *Jasus edwardsii* off the New Zealand coast. They also conclude that geostrophic advection alone cannot explain the presence of lobsters at the coast and suggest that larvae may develop swimming capabilities at an earlier stage than has previously been demonstrated.

1.5. RESEARCH CHAPTERS

This thesis is concerned with literature study, data analysis and the development and evaluation of models for the physiology, behaviour and spatial dynamics of tunas in relation to their oceanic environment. Following this introduction there are 4 research chapters, reflecting the different components of the study undertaken. In Chapter 2, exploratory data analysis is carried out on a 6 yr time series of observed catch data from surface longline fisheries in New Zealand waters in order to determine scales at which tunas are aggregated. In Chapter 3, various models for the physiology and sensory biology of tunas are developed from the available literature. These are then used as components of behavioural (Chapter 4) and life history (Chapter 5) models. In Chapter 6 the individual components detailed in the preceding research chapters are brought together in a general discussion and the main conclusions of this study are presented.

1.6. PEER-REVIEWED PAPERS

Much of this thesis has been submitted, in the form of papers, to peer-reviewed publications:

1. Kirby DS, Hart PJB (1998) A dynamic optimisation model for the behaviour of tunas at ocean fronts. EOS Trans Am Geophys Union, 79:1, Ocean sciences meeting suppl. OS53 (abstract only)

2. Kirby DS, Fiksen Ø, Hart PJB (2000) A dynamic optimisation model for the behaviour of tunas at ocean fronts. Fish Oceanogr 9(4):328–342

3. Kirby DS (in press) Remote sensing and fisheries applications: an overview. In: Morales J (ed) Scientific and operational applications of remote sensing and integrated information systems for coastal and marine fisheries. Coastal region & small island papers, UNESCO, Paris

4. Kirby DS (2001) On the integrated study of tuna behaviour and spatial dynamics: tagging and modelling as complementary tools. In: Sibert JR, Nielsen J (eds) Electronic tagging and tracking in marine fisheries. Kluwer Academic Publishers, The Netherlands, p 407–420

5. Kirby DS, Abraham ER, Uddstrom MJ, Dean H (submitted) Tuna aggregations observed in surface longline data 1993-8. Can J Fish Aquat Sci

6. Kirby DS, Huse G, Lehodey P, Hart PJB (in prep.) A spatial life history model for Pacific skipjack tuna *Katsuwonas pelamis*.

CHAPTER 2

TUNA AGGREGATIONS OBSERVED
IN SURFACE LONGLINE DATA 1993 to 1998

CONTENTS

2.1. SUMMARY

This work was carried out from Feb 1999 to Sep 2000, while I was working as a Visiting Scientist on the Remote Sensing for Fisheries Programme at the National Institute of Water and Atmospheric Research (NIWA), Wellington, New Zealand. The purpose of the project as a whole is to develop satellite-based forecasting systems for the NZ tuna fishing industry. Exploratory data analysis was carried out as a pre-cursor to the development of empirical models attempting to relate patterns in fish catch distributions to oceanographic features apparent in satellite data. A high resolution (hook-by-hook), 6 yr time series of observed longline catch data for tunas was used to investigate fine-scale spatial patterns along individual sets that may be indicative of social behaviour (i.e. schooling) and/or the response of individual fish to favourable extrinsic conditions (i.e. aggregation). Distinguishing between these patterns and understanding the processes that contribute to their formation is likely to enable better forecasting of fish distributions in relation to satellite data. Methods of spatial data analysis (nearest neighbour analysis) that have previously been applied in other sciences (e.g. forestry & astronomy) were used here. Mean Nearest Neighbour Distances (NNDs) are found to be 100–200 m, compared with 200–700 m predicted by a non-homogeneous Poisson process on the same sample space. In addition, I decided to calculate the furthest distance between species of interest, in order to estimate the largest scale within which tunas are aggregated. Mean Furthest Neighbour Distances (FNDs) are between 20 and 50 km, compared to the range of 10 to 20 km predicted by the Poisson process, and to the length of the longlines (50–150 km). The results for NNDs imply that these adult tunas may actually be schooling, while the results for FNDs suggest that these schools are aggregated within scales that may relate to mesoscale oceanographic processes. Further investigation to identify favourable habitat characteristics should therefore focus on the biophysical and trophic dynamics at the sub-mesoscale (50–100 km). This is the first time that such fine-scale analysis has been carried out for pelagic longline catch data using such a large dataset.

2.2. INTRODUCTION

Questions concerning how and why fish use the space available to them in the oceans are central to understanding the ecological interactions that impact on marine fisheries. For high-value, low catch-per-unit-effort (CPUE, see 2.3.1) fisheries, these questions assume even greater importance. Sharp (1978) estimated that if yellowfin tuna in the eastern tropical Pacific were randomly and uniformly distributed there would only be one 10 kg fish per 2.8 km^2 of ocean. He concluded that 'If tunas were truly uniformly distributed in their habitat they would be so rarely encountered as to be virtually non-existent.' Some species of tuna are normally found in association with many other conspecifics e.g. skipjack (Bayliff 1988, Hilborn 1991), yellowfin (Klimley & Holloway 1999), and young albacore (Laurs et al. 1984), while others are thought to be solitary, at least when not forming spawning aggregations (Winkler et al. 1983) e.g. older albacore, bigeye and adult northern and southern bluefin. The degree of association between con-specifics is of great relevance to fisheries, as it will clearly determine gear type and/or the timing and location of effort. In New Zealand tuna fisheries, schools of skipjack and young albacore are targeted with seine nets and trolling gear respectively, while adult southern bluefin, bigeye and yellowfin are targeted by surface longlines. The degree of association between con-specifics is determined by a number of factors, both intrinsic (i.e. evolved behaviour) and extrinsic (i.e. response to environmental conditions). The ways in which marine predators respond to their environment are likely to be scale-dependent, and if variability in population density has a characteristic spatial scale, subsequent research to determine the conditions favouring aggregation can focus on this scale (Schneider 1994). In this chapter. I explore the spatial patterns that exist in longline catch data for tunas at the finest scale possible. By identifying fine scale patterns, we begin to find out more about both social behaviour and interactions between fish and environment. It may then become possible to use such knowledge for monitoring and prediction in the fishery.

2.2.1. Definition of terms

Various terms are used in the behavioural ecology and fisheries literature to describe spatial patterns observed in animal distributions. Schooling, shoaling, clustering, aggregating and congregating are all terms that have been deployed, often inter-changeably, to describe non-uniform or apparently non-random spatial patterns. These words may describe similar patterns but it is useful to let them have different meanings, in order to distinguish the different causes that can have the same effect. Fish may come together in order to minimise predation risk or to maximise encounter rates with prey or potential mates (Pitcher & Parrish 1993). This bio-social attraction is best considered as schooling or shoaling. Individuals may also come together as a direct response to extrinsic environmental conditions. Such behaviour is best termed aggregation. Individuals are considered to be acting independently of each other, and are instead responding in a similar way to some other factor or combination of factors, e.g. prey density.

2.2.2. Observed longline catch data

Under the New Zealand Ministry of Fisheries Scientific Observer Programme, an observer is placed on board all visiting foreign licensed surface longline vessels and also a percentage of domestic licensed vessels. The fisheries target large adult tunas of 2 species: Southern Bluefin (STN) and Bigeye (BIG). Albacore (ALB) and Yellowfin (YFN) are not formally targeted but are a significant and saleable bycatch. Surface longline fishing vessels follow a general pattern of operation over a 24 h period. Larger vessels set the fishing gear in the early hours of the morning to soak the baits during the hours preceding dawn. This operation usually requires 4–8 h and may be followed by 4–5 h of waiting before the gear is retrieved, although longer lines may be retrieved after a shorter interval. The catch is processed during the next 12 h. The whole operation is quicker for the smaller vessels of the domestic fleet. A large vessel will set 120–150 km of longline; smaller vessels set 40–80 km of line. From the longline, 2500–3500 snood lines are suspended, each with a single baited

hook. Emphasis is placed on getting good information on catch, rather than on the setting operation. The main aspects of the setting operation are nevertheless recorded, including start and finish times and positions, the number of hooks, length of line set, vessel speed, line feeder speed, distance between marker buoys, number of baskets, and basic weather information. At the start and finish of the haul, and at hourly intervals throughout, time and position and basic weather information are recorded. As each specimen is landed on deck, the time is recorded and the specimen identified, weighed, measured and sexed. Positions of each landed specimen are subsequently determined as follows:

1. An array representing all hooks is constructed with blank position and time details.

2. The first hook is assigned the start-of-haul position and time, and the last hook is assigned the end-of-haul position.

3. Times are calculated for every other hook, assuming a constant speed while hauling.

4. Hooks closest in time to the hourly haul records are flagged.

5. Between each hook flagged with an hourly haul position, the position of each intervening hook is interpolated by great circle path navigation, using the time assigned.

6. Each recorded specimen is placed on the hook closest to its recorded landing time; if that hook is already occupied, the specimen is placed on the nearest unoccupied hook.

2.2.3. Hypothesis generation

Where point events of interest occur completely at random within a sample space, this can be formally described as a Poisson process. The presence or absence of an event at a particular location is not influenced by any other event, and if the process is homogeneous, no part of the sample space is any more likely to contain point events than another. A non-homogeneous Poisson process allows for such variation, but the events themselves are still independent. Such processes provide a base against which to compare other processes where either clustering or inhibition of events are thought to occur (Cox et al. 2000).

Tunas are not randomly distributed throughout New Zealand waters all year round. We would expect this from a basic understanding of ocean biogeography and the evolution of fish life histories. The largest scale at which this non-homogeneity is apparent can be inferred from the areas where fishers have come to target their effort (Fig. 2.1). Detailed analysis of individual fishing sets shows that even after deliberate targeting by experienced fishers, CPUE is still an over-dispersed quantity, i.e. variance is greater than the mean (Fig. 2.2 and Richardson et al. submitted). We can therefore view CPUE for tunas as being the result of a non-homogeneous Poisson process, whereby different areas, within the larger area of preferred habitat, are more likely to contain more fish, but where the occurrence of each individual is independent of the occurrence of another. We can test this hypothesis by measuring the distances between individual fish in the observed catch data, and comparing the frequency distribution of these distances with the distribution that results from a non-homogeneous Poisson process. If the fish are found to be randomly distributed along the set, then the set scale (50–150km) is the finest scale at which they can be considered aggregated, and the targeting of research and fishing effort should focus on this scale. But if they are aggregated *within* the scale of the set, we should focus on the environmental heterogeneity that may exist on this smaller scale for an explanation of their spatial dynamics. Our hypothesis is therefore that tunas are aggregated relative to a random distribution along a set, and we seek to identify the spatial scale or scales at which such aggregations occur.

Fig. 2.1 Locations of observed surface longline sets in New Zealand waters 1993 to 1998, targeting (a) southern bluefin STN and (b) bigeye BIG
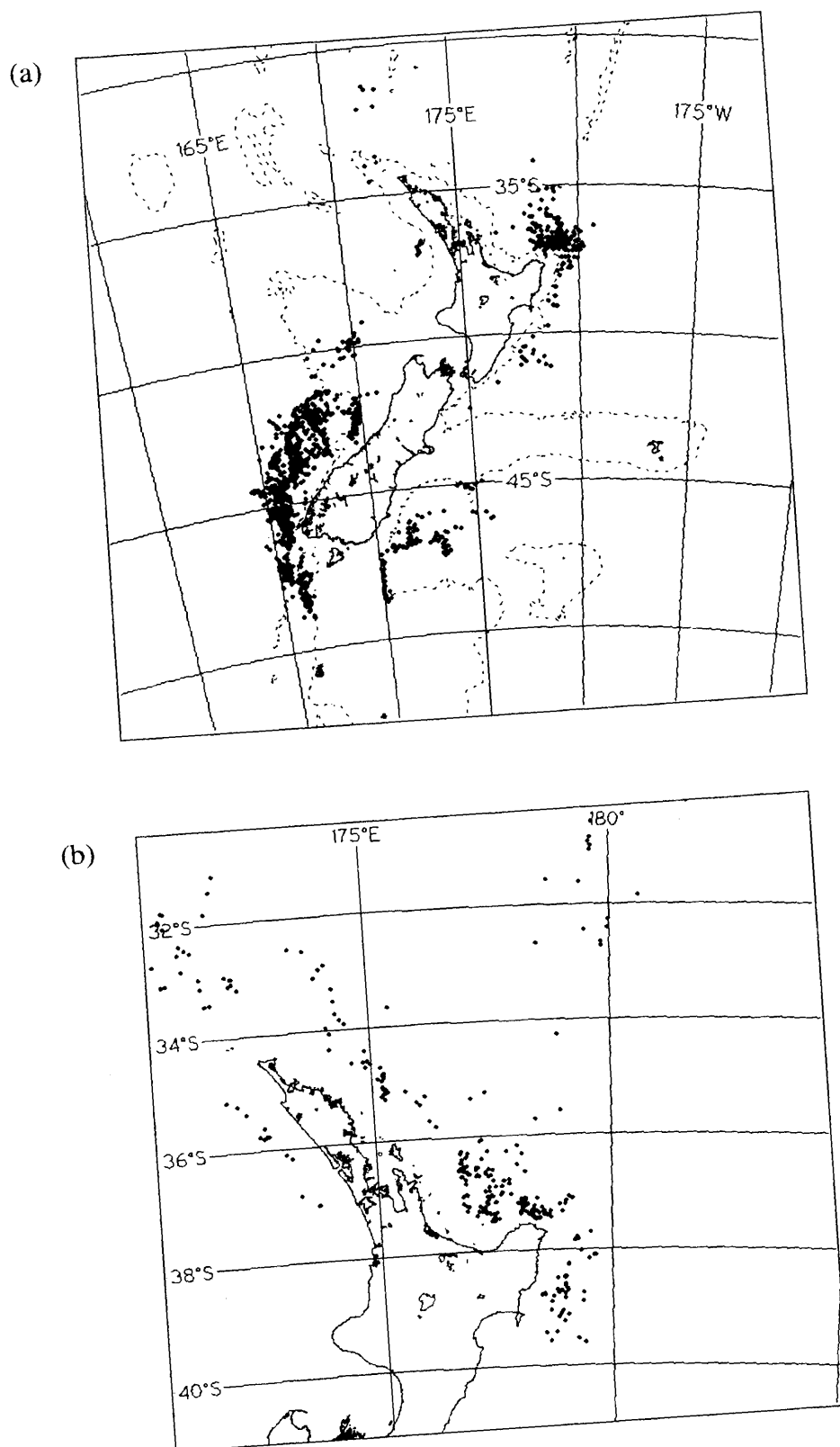
2.3. DATA ANALYSIS

Fields of interest were extracted from the MFish database held at NIWA Wellington, and the positions of individual fish were calculated as described above. ASCII files were generated detailing this information, and the analysis described below was then carried out.

2.3.1. Nominal catch-per-unit-effort (CPUE)

CPUE for surface longline fisheries is nominally defined as the number of fish caught per thousand hooks. There are many factors that can determine the likelihood of a particular hook catching a fish, including depth of the hook, bait type, and of course the timing and location of effort. Nominal CPUE is therefore only a gross measure of relative abundance that may confound the effects of contributing factors. Fishing is also as much a non-random method of sampling as the fisher can make it. For the purpose of the analysis presented here, where we are interested primarily in the locations of point events, no estimate has been made of the effectiveness of fishing effort. Implicit in the analysis is the assumption that all hooks have the same likelihood of catching a subject should one be present at that point during the fishing period. This may not be the case in reality. This does not undermine the analysis because we are primarily concerned with discovering aggregations within the scale of the set, rather than identifying causes of variation in CPUE between sets. If no aggregations were apparent, we would conclude that fishers are targeting effort as efficiently as possible, and that the finest scale on which tunas may be considered aggregated is that of the set itself.

2.3.2. Set-scale probabilities

For target species, the probability of catching at least 1 fish represents the extent of fishers' prior knowledge, i.e. how well they are targeting areas preferred by the fish. For all species, the probability of catching more than 1 subject, and the conditional probability of catching an additional subject having already caught a first, are preliminary measures of fish aggregation on the scale of the set.

Fig. 2.2 Frequency distributions of nominal CPUE (catch/1000 hooks) for observed surface longline sets in New Zealand waters 1993–8, by Subject Species, Target Species and Area. Species codes as given on p 31.
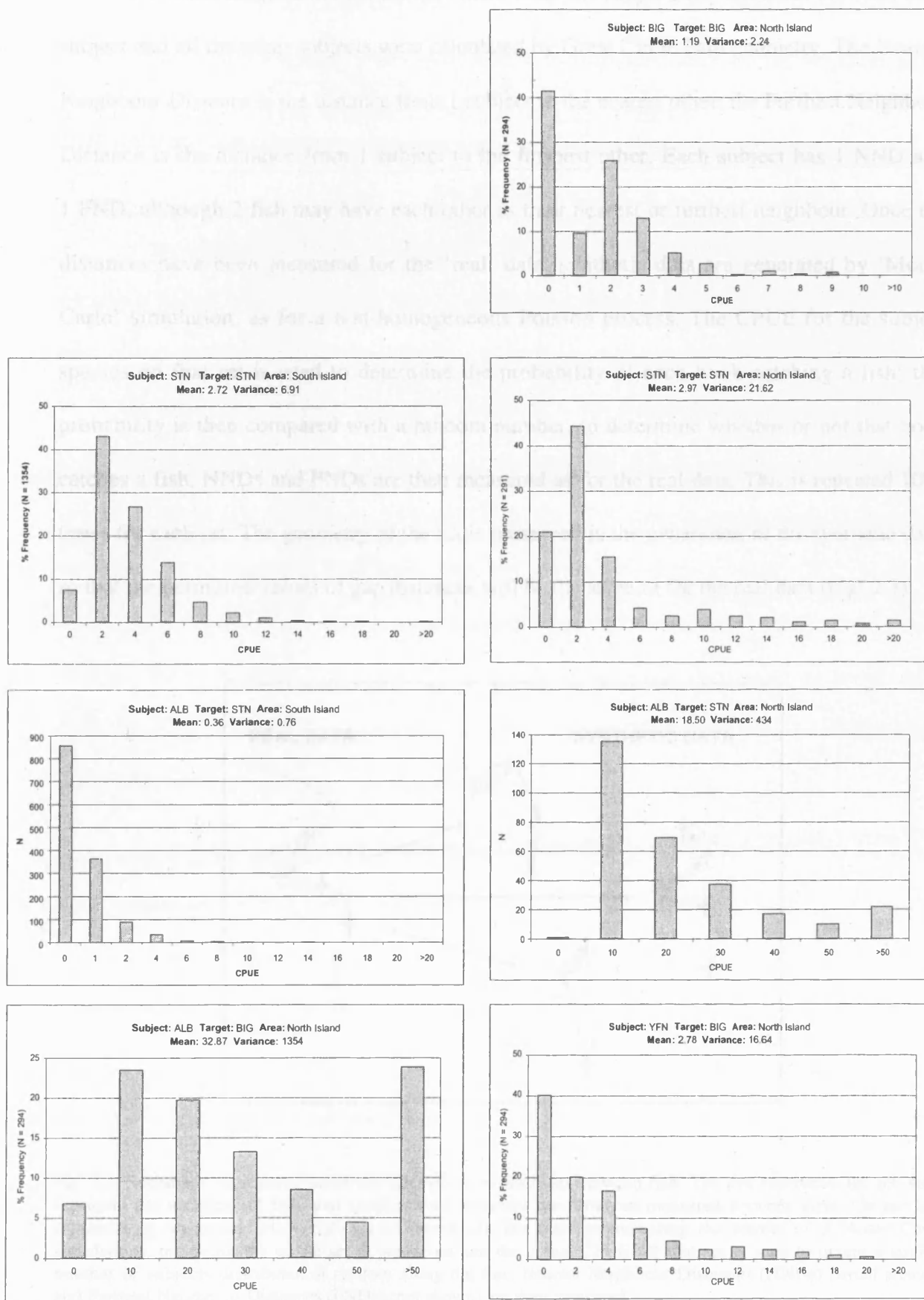
2.3.3. Nearest & furthest neighbour distances

For each longline set that caught more than one subject, the distances between each subject and all the other subjects were calculated by Great Circle Path geometry. The Nearest Neighbour Distance is the distance from 1 subject to the nearest other; the Furthest Neighbour Distance is the distance from 1 subject to the furthest other. Each subject has 1 NND and 1 FND, although 2 fish may have each other as their nearest or furthest neighbour. Once the distances have been measured for the 'real' data, synthetic data are generated by 'Monte Carlo' simulation, as for a non-homogeneous Poisson process. The CPUE for the subject species on that set is used to determine the probability of each hook catching a fish; this probability is then compared with a random number, to determine whether or not that hook catches a fish. NNDs and FNDs are then measured as for the real data. This is repeated 1000 times for each set. The geometry of the set is preserved in the generation of the synthetic data, so that the permitted values of gap distances will be the same as for the real data (Fig. 2.3).
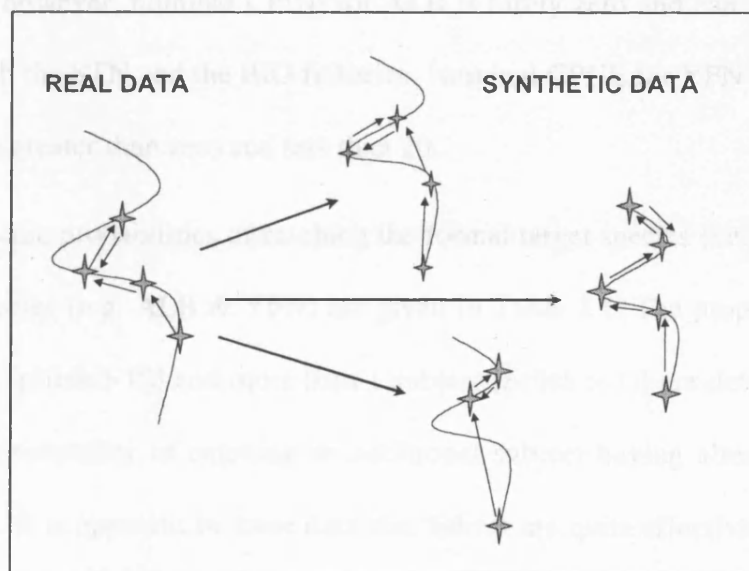
Fig. 2.3 Schematic representation of the calculation of distances between fish. The line represents the set, stars represent the locations of fish, and small arrows represent the distances measured between them. On the left, representing an actual set, 4 fish are clustered. On the right, representing the results of 3 Monte Carlo simulations, the geometry of the set is preserved and the actual CPUE for that set is used to obtain a similar number of subjects distributed at random along the line. Nearest Neighbour Distances (NNDs) (small arrows) and Furthest Neighbour Distances (FNDs) (not shown) are then measured

The CPUE for each set is used in preference to the aggregated mean for the fishery, bearing in mind that '...what is considered to be a clustered pattern with the assumption of homogeneity in force could also be the result of heterogeneity' (Ripley 1981). This reduces our chances of Type 1 error, where we might believe that there is aggregation *within* the set, when the effect is in fact caused by spatial variation in CPUE *at the scale of* the set.

2:4. RESULTS

Frequency histograms of nominal CPUE for the data used in this analysis are presented in Fig. 2.2. For the BIG fishery, which takes place in the warm waters off the north-eastern region (Fig. 2.1), nominal CPUE is most frequently zero, with occasional catches up to 10 fish per thousand hooks. For the STN fishery in northern waters, nominal CPUE is also most frequently low (<2), but in 10% of cases nominal CPUE is at least 10, and in a few cases is at least 20. In southern waters, nominal CPUE for STN is rarely greater than 10, but there are less cases of nominal CPUE being zero, and more cases where nominal CPUE is greater than 2. Nominal CPUE for ALB is most frequently zero and always low in southern waters. In northern waters however, nominal CPUE for ALB is rarely zero and can be extremely high (>50 fish) in both the STN and the BIG fisheries. Nominal CPUE for YFN is most frequently zero, but is often greater than zero and less than 20.

The set-scale probabilities of catching the formal target species (i.e. STN or BIG) and other subject species (e.g. ALB & YFN) are given in Table 2.1. The proportion of sets that caught at least 1 [p(fish > 0)] and more than 1 subject [p(fish > 1)] are detailed, followed by the conditional probability of catching an additional subject having already caught a first [p(fish2 | fish1)]. It is apparent in these data that fishers are quite effective at targeting STN [p(STN) ≈ 80–90%] and that these are not usually found alone [p(STN2 | STN1) ≈ 90%]. When BIG are targeted, the probability of catching at least 1 target is much lower [p(BIG) ≈ 60%] and there is only a 50% chance of catching another BIG on the same set.

Table 2.1 Set-scale probabilities for catching at least 1 subject, more than 1 subject, and conditional probability of catching a second subject having caught a first. The mean number of subjects caught on the subset of longlines with 2 or more subjects, their mean Nearest Neighbour Distances (NND), and the mean NNDs for the Poisson process are are then reported. Mean Aggregation Index (AI) is calculated as: (1 − meanNND/meanRanNND), and scales between −1 and 1; values near 1 indicate strong aggregation. Mean Furthest Neighbour Distances (FNDs) are a measure of the maximum scale within the sample space of the longline within which the subject species is present

Subject Species	Target Species	Area (Island)	p(fish > 0)	p(fish > 1)	p(fish2 | fish1)	Mean N(fish)	Mean NND (m)	Mean RanNND (m)	Mean AI	Mean FND (km)	Mean RanFND (km)
BIG	BIG	NORTH	0.59	0.31	0.52	4	97	279	0.63	22.1	10.3
STN	STN	NORTH	0.79	0.67	0.85	12	156	560	0.67	38.2	17.3
STN	STN	SOUTH	0.93	0.84	0.91	10	170	652	0.71	50.4	21.8
ALB	STN	NORTH	1.00	0.99	0.99	39	155	465	0.63	54.4	22.0
ALB	BIG	NORTH	0.99	0.98	0.99	37	72	267	0.70	28.1	11.2
ALB	STN	SOUTH	0.37	0.18	0.50	4	163	557	0.69	36.1	16.7
YFN	BIG	NORTH	0.60	0.41	0.69	6	71	205	0.61	17.5	7.3

The probability of catching at least 1 YFN is the same as for the formal target species BIG [p(YFN) ≈ p(BIG) ≈ 60%], but it is more likely that more than 1 YFN will be caught on the same set [p(YFN2 | YFN1) ≈ 70%]. ALB are apparently ubiquitous in both the BIG and STN fisheries off the North Island [p(ALB) ≈ 100%; p(ALB2 | ALB1) ≈ 100%]. This provides fishers with their basic income, which is then supplemented by less frequent but more lucrative catches of the target species. ALB are caught less frequently in the longline fisheries off the South Island [p(ALB) ≈ 40%], where they are often caught on their own [p(ALB2 | ALB1) = 50%]. There are separate fisheries for younger Albacore in these waters that are able to target discrete schools using trolling gear.

For each species, NND and FND calculations were carried out for sets that caught more than 1 subject; the mean number of fish in this subsample is listed. The NNDs are generally around 100 m, which is the same order of magnitude but 25–50% shorter than the NNDs resulting from the Poisson process (RanNND). The frequency distributions for the real and synthetic data are presented in Fig. 2.4. In all cases the NNDs are skewed to the shorter distances, mostly less than 200 m. If the subjects were distributed randomly along the set, as they are in the synthetic data, the NNDs would be more variable and generally greater.

Fig. 2.4 Frequency distributions for Nearest Neighbour Distances (NNDs) by Subject species, Target species and Area.
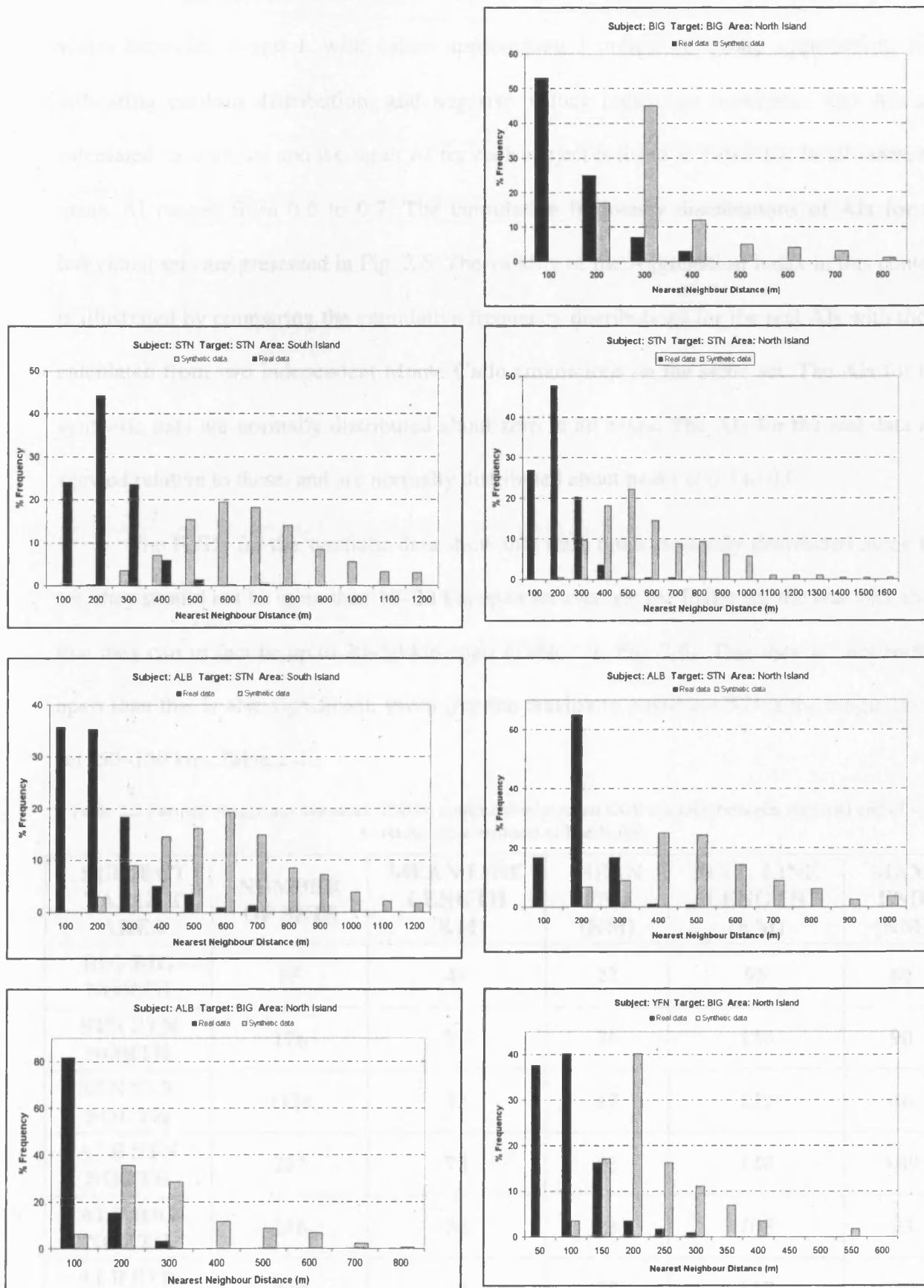
An Aggregation Index (AI) was defined as: 1 − (mean NND/mean RanNND). This scales between −1 and 1, with values approaching 1 indicating strong aggregation, zero indicating random distribution, and negative values indicating repulsion. The AIs are calculated for each set and the mean AI for each subject is listed in Table 2.1. In all cases, the mean AI ranges from 0.6 to 0.7. The cumulative frequency distributions of AIs for all individual sets are presented in Fig. 2.5. The validity of the Aggregation Index in this context is illustrated by comparing the cumulative frequency distributions for the real AIs with those calculated from two independent Monte Carlo simulations on the same set. The AIs for the synthetic data are normally distributed about zero in all cases. The AIs for the real data are skewed relative to these, and are normally distributed about peaks at 0.3 to 0.6.

The FNDs for the synthetic data show that were tunas randomly distributed along the set, they should not be more than 10–20 km apart on average; the FNDs for the real data show that they can in fact be up to 20–50 km apart (Table 2.1, Fig. 2.6). That they are not further apart than this is also significant, given that the maximum possible FND is the length of the set (50–150 km; Table 2.2).

Table 2.2 Furthest neighbour distances (FNDs) compared with mean GCP distance between start and end of set, a conservative estimate of line length

SUBJECT TARGET AREA	NUMBER OF SETS	MEAN LINE LENGTH (KM)	MEAN FND (KM)	MAX. LINE LENGTH (KM)	MAX. FND (KM)
BIG BIG NORTH	85	49	22	95	82
STN STN NORTH	176	75	36	130	90
STN STN SOUTH	1126	73	17	132	46
ALB STN NORTH	257	73	53	140	109
ALB BIG NORTH	256	38	28	105	93
ALB STN SOUTH	222	72	35	117	101
YFN BIG	112	33	17	91	46

Fig. 2.5 Cumulative frequency distributions for Aggregation Index (AI) by Subject Species, Target Species and Area
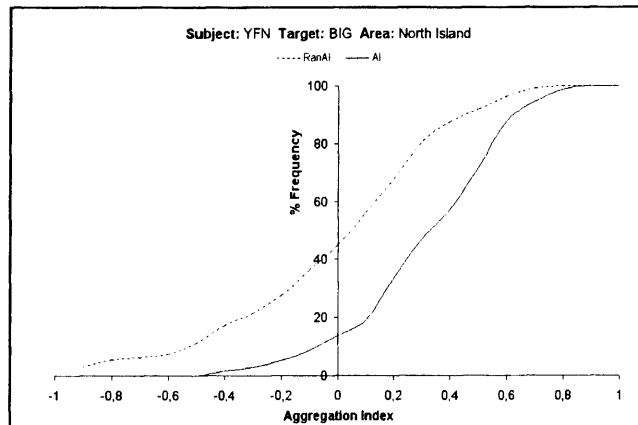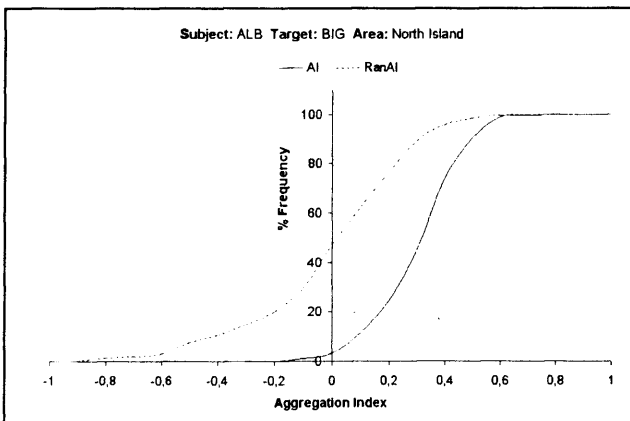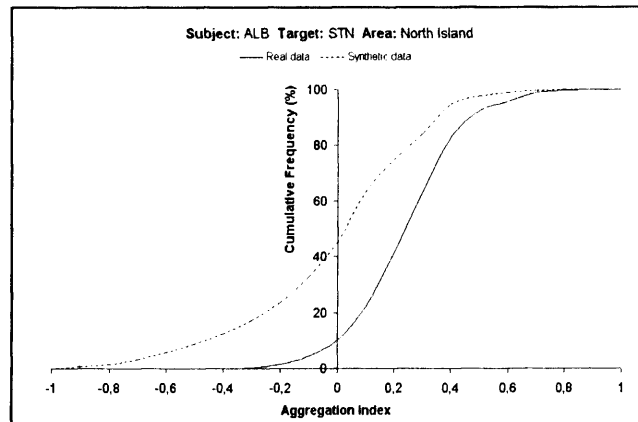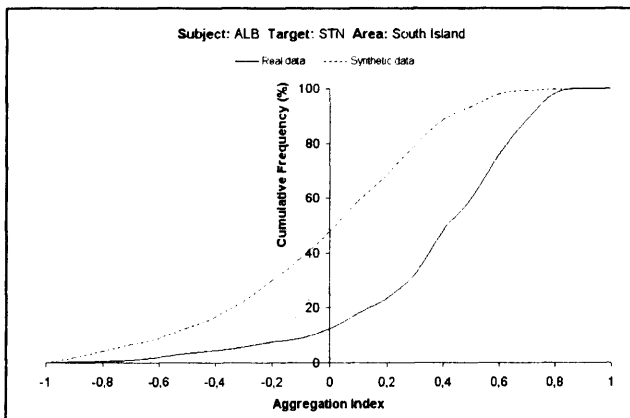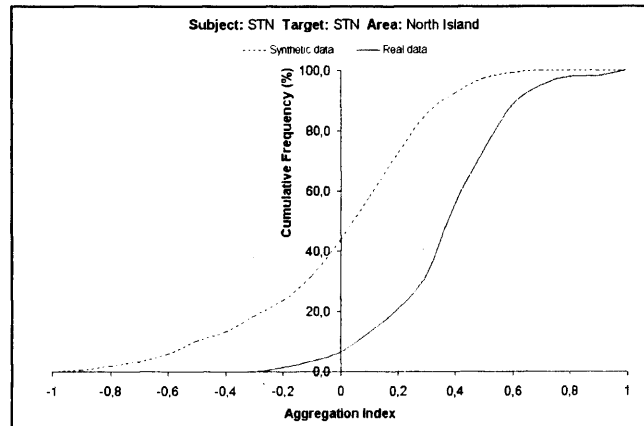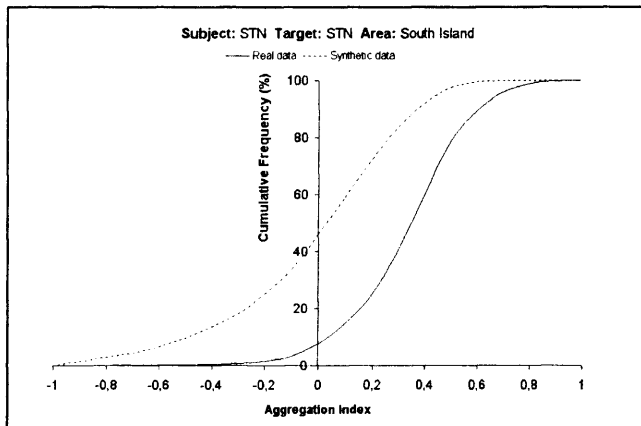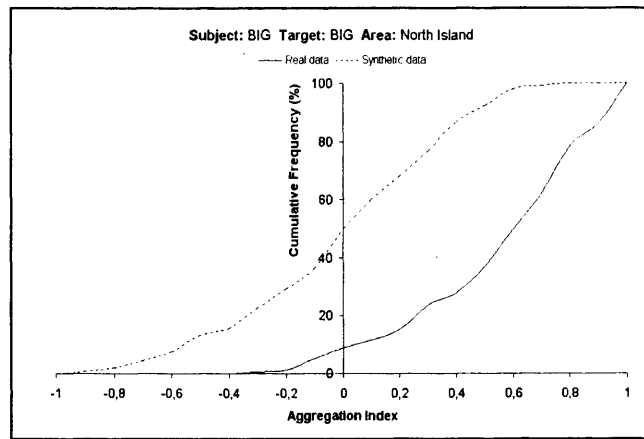
Fig. 2.6 Frequency distributions for Furthest Neighbour Distances (FNDs) by Subject Species, Target species and Area
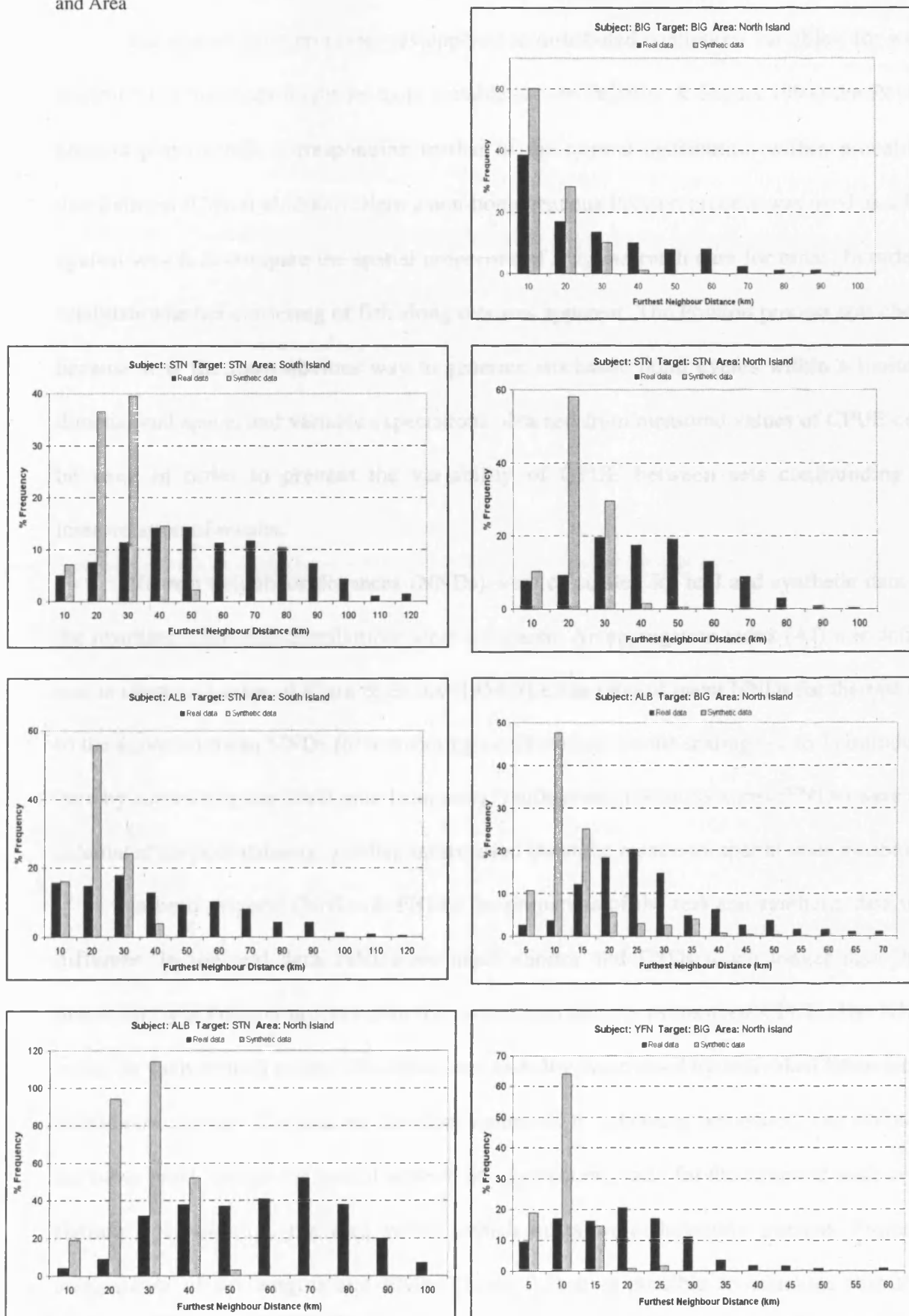
2.5. DISCUSSION

For spatial point processes (as opposed to distributed continuous variables, for which geostatistical methods might be more suitable — see Pelletier & Parma 1994) the Poisson process plays a role corresponding to that of the normal distribution within probability distributions (Cox et al. 2000). Here a non-homogeneous Poisson process was used as a base against which to compare the spatial properties of longline catch data for tunas, in order to establish whether clustering of fish along sets was apparent. The Poisson process was chosen because it is the most obvious way to generate stochastic point events within a limited 2 dimensional space, and variable expectations obtained from measured values of CPUE could be used in order to prevent the variability of CPUE between sets confounding the interpretation of results.

Nearest neighbour distances (NNDs) were calculated for real and synthetic data and the resulting frequency distributions were compared. An aggregation index (AI) was defined that is identical to that of Clark & Evans (1954) (i.e. the ratio of mean NNDs for the real data to the expected mean NNDs for a random process) except for the scaling (–1 to 1) introduced here by subtracting the NND ratio from unity. Furthest neighbour distances (FNDs) were also calculated for both datasets, yielding information about the maximum spatial scale inhabited.

In both respects (NNDs & FNDs) the properties of the real and synthetic data were different. In the real data, NNDs are much shorter and FNDs much longer than those predicted by a Poisson process with the same heterogeneity as nominal CPUE. The NNDs, being on such a small scale (100–200m) are probably determined by individual behaviour in relation to con-specifics and are therefore indicative of schooling behaviour. The FNDs, on the other hand, denote the spatial scale of an aggregation, valid for the temporal scale of the fishing operation i.e. the area within which tunas were definitely present. From the comparison of set lengths and FNDs (Table 2.2) it is possible to conclude that these aggregations are often within a sub-mesoscale area that is smaller than the scale of the set. The FNDs may relate to mesoscale and sub-mesoscale oceanographic features and processes

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that have concentrated tuna prey (i.e. micronekton), which may present an odour field to which tunas respond.

Adult tunas may therefore be more social than has traditionally been thought. However, we should recall that NND and FND analysis has only been carried out for sets where >1 subject was caught; the results must be interpreted alongside the set-scale probabilities for catching 1 and >1 fish. An alternative interpretation would be that favourable microhabitats at the scale of the NNDs have been sampled, within the larger area of unfavourable habitat represented by the scale of the set. The distribution of tuna prey is indeed likely to be patchy, and shoals of forage fish may have diameters similar to the NNDs. However, tunas are more highly mobile than their prey and are not likely to be phase-locked with them in time and space. They have to cross comparatively empty space in between prey encounters and would be more likely to take a baited hook during this time than when they are feeding on a shoal of forage fish. The microhabitat hypothesis becomes more implausible when one considers the scale of physical features in the ocean that might enhance habitat and be attractive to tunas — ocean processes on scales of 100–200 m are not likely to have an effect on habitat suitability for large pelagic predators. It is also possible that tunas are conducting non-trophic migrations through New Zealand waters and that proximate environmental conditions are to be endured whether or not they especially favourable.

Data have only been considered in the horizontal dimension, while longline fishing gear is targeted at tunas with varying and variable depth preferences. Longlines are set deeper for BIG, therefore they are shorter for the same gear/vessel that might previously have been fishing for STN. The volume of data analysed here prevents detailed consideration of these factors but the analysis has been stratified by target species and area for this reason. Considering some hypothetical scenarios, clusters of catches might be apparent along a fishing line that was only effectively targeting tuna habitat with e.g. the deepest hooks. The spacing of such clusters would be comparable to the distance between surface floats.

Alternatively, hooks at intermediate depth might be most effective; in this case the there might be 2 clusters in between floats. The average distance between floats is 340 m. The NNDs are shorter and the FNDs longer than this. The behaviour of fish that have been caught might modify the potential for nearby hooks to catch fish; such a tendency would, however, make aggregations less, rather than more likely. Similarly, a school of fish might swim along the line and so catches might then appear to be randomly distributed, i.e. they could occur along the line with equal likelihood. Such behaviour would indeed result in spatial patterns analagous to those produced by the Poisson process; aggregation index as we have defined it here would therefore be zero (as shown in Fig. 2.5). But such behaviour is allowed for in our definition of aggregation as being FNDs smaller than the maximum length scale available (i.e. the length of the set). That much closer clusters are also detected along the set (i.e. NNDs shorter than if the catches were randomly distributed) indicates that within the larger scale aggregation there is finer scale schooling.

The presence of fish other than tuna (i.e. fish bycatch) would interfere with the data in that a hook that has already been taken by a shark, for example, would no longer be available to a tuna. Although it is the case that the majority of the total fish catch on a longline is bycatch, it is also the case that the majority of hooks do not catch anything at all (Francis et al. 2000). It is therefore unlikely that there is any systematic bias in the data due to bycatch.

Issues concerning spatial and temporal scale arise frequently in discussions on the behaviour and spatial dynamics of tunas (Hunter et al. 1980). Tagging studies often report either long-distance movements or fine-scale behaviour (Kirby 2001), but behaviour in relation to con-specifics has rarely been reported. We still struggle with how to use knowledge of physiology and behaviour in order to understand movement patterns and population dynamics. Modelling studies have tried to address the conditions under which school formation may occur, based on food intake requirements (Dagorn et al. 1995), swimming efficiency (Stocker 2000) and social interaction (Dagorn & Freon 1999).

The real world is always more complicated than a model, and fisheries data are fraught with imperfections; here we can do little more than speculatively transfer ideas between model and natural environments. The animals forming the basis of this study were, until the time of capture at least, sensing and moving through their natural environment in the search for food, driven by the need to grow, stay healthy and reproduce. Further work might try to assess in more detail the factors motivating their behaviour and spatial dynamics, with the understanding that such knowledge would prove useful in the management of tuna resources. Specifically, the trophic dynamics of fishing grounds should be investigated (e.g. Roger 1994, Young et al. 1996a, 1996b, 1997) in relation to observations of surface oceanography (e.g. Uddstrom & Oien 1999, McClatchie & Coombs submitted). Experimental fishing, with simultaneous measurement of in situ variables, would start to address cause and effect relationships determining the relative adundance of tunas. Such an exercise would also reduce uncertainty in hook locations and would allow hook depth to be included in the analysis.

2.6. CONCLUSIONS

CPUE for tunas in surface longline fisheries in New Zealand waters varies throughout the EEZ. It varies greatly between fishing sets even after targeting of key species by experienced fishers. A possible reason for this is that tunas are not randomly distributed throughout the EEZ, or even on finer scales such as the fishing areas targetted or along the fishing lines set. This work has determined that they are in fact patchily distributed, and has determined the scales at which this occurs. Tunas in New Zealand waters are forming loose schools, on the scale of 100–200m between individual fish, that are in turn aggregated over length scales of 20–50 km. The motivations for these aggregations (i.e. the environmental properties that are independently attractive to many individual tuna) have not been determined in this study, but they may be a direct response to local prey concentrations, which in turn may be the result of local ocean dynamics and enrichment processes at scales less than 100 km, i.e. sub-mesoscale. Further research to investigate these hypotheses is strongly advocated, with sampling focussed on the biophysical and trophic dynamics at these scales.

CHAPTER 3

TUNA PHYSIOLOGY AND SENSORY BIOLOGY

CONTENTS

3.1. SUMMARY

This chapter represents a quantitative synthesis of available knowledge on the physiology and sensory biology of tunas. It is based on a comprehensive review of the relevant literature and also includes the development and application of analytical models. Vision, olfaction, bioenergetics and thermal stress are examined, which allows reaction distances and vital rates to be used in the behavioural and life history models presented later (Chapters 4 & 5 respectively).

3.2. REACTION DISTANCES

The detection and location of prey are key processes determining habitat selection and the spatial distribution of predators. Tunas are highly visual predators (Nakamura 1967, Kawamura et al. 1981), yet they also have a well developed nose and olfactory nerve (Gooding 1962, in Atema et al. 1980), which is likely to enable detection and identification of prey at a distance, prior to visual search, prey location and final attack (Atema 1980, Atema et al. 1980). The reaction distances enabled by these sensory systems have never been reported for tuna. Reaction distances are important components of foraging models (Kirby et al. 2000, Chapter 4) and of ecological processes in general. They will determine encounter rates and habitat profitability, energy budgets and transfer rates, and so play a significant role in oceanic ecosystems. The lack of information on reaction distances is therefore a significant barrier to better understanding of tuna species. In this chapter, and in order to develop the foraging and life history models detailed later in this theseis (Chapters 4 & 5 respectively), I have taken what information is available in the literature and attempted to calculate reaction distances for prey detection by vision and olfaction. The essential parameters relevant to the calculation of visual range and different methods for their determination are briefly discussed. Different approaches to calculating visual range itself are also considered. Previous experimental work and new considerations of the dispersion of tracers in the surface ocean are used to estimate reaction distances for prey detection by olfaction.

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3.2.1. Visual range

Visual range depends on the ability of the eye to detect and resolve objects; pattern recognition and prey selection may then follow. Visual acuity is normally defined as the minimum angle which a stimulus can subtend at the eye and yet still be resolved. It can be determined either theoretically, by means of histological measurements of cone density at the retina of the eye, or behaviourally, by determining the smallest stimulus size that will elicit a partcular response. Such determinations have been made for tunas (Nakamura 1967, Kawamura et al. 1981, Table 3.1).

Table 3.1 Minimum separable angle and maximum visual acuity for tuna eyes. Methods: 1 = histology (Kawamura et al. 1981); 2 = experiment (Nakamura 1968); 3 = experiment (Nakamura 1967)

Species	Fork length (cm)	Method / reference	Minimum separable angle (minutes of arc)	Maximum visual acuity (1 / min. separable angle)
Albacore	97	1	2.09	0.48
	105	1	2.04	0.49
Bigeye	111	1	2.52	0.40
	139	1	2.27	0.44
Bluefin	120	1	3.57	0.28
	52	1	3.67	0.27
Skipjack	–	2	5.56	0.180
Yellowfin	49 & 59	3	3.65	0.274
	105	1	2.06	0.49

Visual acuity for tunas (Table 3.1) is the highest among fishes and their retinae are considered to be particularly well adapted for movement perception (Kawamura et al. 1981). Within tuna species, the larger fish tends to have better acuity (with the exception of Bluefin). This is consistent with the general consensus that fish eyes continue to grow (asymptotically) throughout life and that acuity increases with increasing eye size (Pankhurst et al. 1993).

The acuity of Albacore, Bigeye and large Yellowfin is high, reflecting their use of deeper waters, while it is lower for the surface-dwelling Skipjack. The low values observed for both small and larger Bluefin are not so consistent with what is understood of their habitat preferences (Chapter 1), although the younger tuna had more numerous single cones than the adult (single cones being lower in sensitivity than double cones or rods) suggesting a shallower habitat for the former (Kawamura et al. 1981). While light intensity at the surface is strong, particularly in the tropics, ambient light is extremely limited below 200 m. The angular distribution of the lightfield at depth is predominantly downward and the spectral distribution is constrained to blue (Jerlov 1970). Colour vision is of no use here but sensitivity is likely to be critical. It is therefore understandable and adaptive that tunas are colourblind and that Yellowfin and Bigeye have maximum spectral sensitivity in the blue (458–492 nm). The highest cone density in tunas was in the ventral retinal region, with the implication that vision is most acute when tunas look upwards (Kawamura et al. 1981). Bigeye, whose physiological adaptations to colder waters are discussed later in this Chapter, also has the largest eye among the tunas and a dense 'tapetum lucidum' in the pigment epithelium layer; this acts as a mirror, increasing the effectiveness of photoreceptors. These adaptations would enable the deeper foraging that is characteristic of this species.

Maximum distance of resolution (i.e. visual range) can be calculated from the minimum separable (also called 'visual') angle as follows (Nakamura 1967): bisection of the visual angle θ yields a right angle; the tangent of half the visual angle, in minutes of arc, equals half the width of the object d, divided by reaction distance r (Fig. 3.1). This is solved for reaction distance thus:

$$r = \frac{(d/2)}{(\tan\{\theta/2\})} \qquad\qquad \text{Eq. 3.1}$$
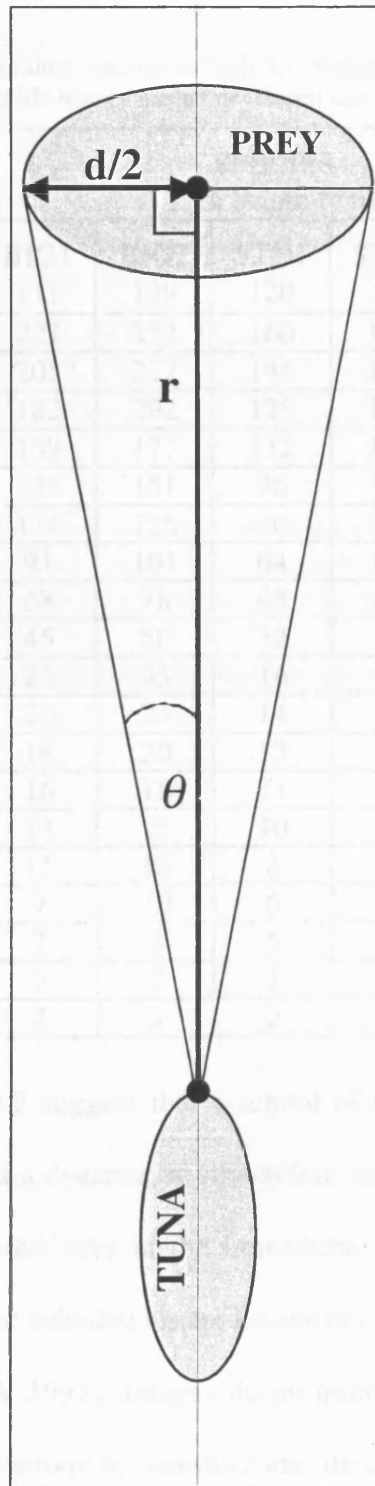
Fig. 3.1 Calculation of visual range using minimum visual angle

The reaction distances calculated by this method are reported in Table 3.2 for the minimum visual angles in Table 3.1.

Table 3.2 Visual range (m) for acuity values reported in Table 3.1. Values for skipjack (bold) used to limit visual range in the foraging and life-history models developed later (Chapters 4 & 5); see p 56

Object diameter (m)	SPECIES fork length (cm)								
	ALB1 97	ALB2 105	BIG1 111	BIG2 139	STN1 120	STN2 52	SKJ –	YFN1/2 49/59	YFN3 105
10	274	281	227	252	160	156	103	157	278
9	247	253	205	227	144	140	93	141	250
8	219	225	182	202	128	125	82	126	222
7	192	197	159	177	112	109	72	110	195
6	164	168	136	151	96	94	62	94	167
5	137	140	114	126	80	78	51	78	139
4	110	112	91	101	64	62	41	63	111
3	82	84	68	76	48	47	**31**	47	83
2	55	56	45	50	32	31	**21**	31	56
1	27	28	23	25	16	16	**10**	16	28
0.9	25	25	20	23	14	14	**9**	14	25
0.8	22	22	18	20	13	12	**8**	13	22
0.7	19	20	16	18	11	11	**7**	11	19
0.6	16	17	14	15	10	9	**6**	9	17
0.5	14	14	11	13	8	8	**5**	8	14
0.4	11	11	9	10	6	6	**4**	6	11
0.3	8	8	7	8	5	5	**3**	5	8
0.2	5	6	5	5	3	3	**2**	3	6
0.1	3	3	2	3	2	2	**1**	2	3

The results in Table 3.2 suggest that a school of fish of 10 m diameter might be detectable to a foraging tuna at a distance of 100–300 m and that an individual prey item of length 10 cm might be detected only in the immediate vicinity (1–3 m) of the crusing predator. However, acuity-based calculations are known to considerably overestimate reaction distances of piscivores (Breck 1993). Images decay quite rapidly underwater because of scattering and absorption of photons by seawater and its constituents. For piscivorous fish searching visually for large prey items, reactive distance is therefore more likely to be limited by contrast than by visual acuity, and to be only minimally dependent on prey size (Eggers 1977, Breck 1993, Giske et al. 1998). Acuity-based calculations are nonetheless useful for at least 'capping' expected visual range for tunas; this is why they have been presented here. A

more detailed mechanistic model for aquatic visual feeding has been derived (Aksnes & Giske 1993, Aksnes & Utne 1997), which includes much detail on the properties of the predator's eye, the optical properties of the water and prey characteristics. These are largely undetermined for tunas and their prey, so in order to derive and apply a model for visual range in relation to the ocean environment, the missing parameters have been collected into a single constant c_1, and visual range varies in relation to water clarity (diffuse attenuation coefficient, k), surface solar irradiance S, and depth z:

$$r^2 \approx c_1 S e^{-kz}$$
Eq. 3.2

When using this model in the foraging and life history models developed later (Chapters 4 & 5), for surface waters visual range r was integrated over the first attenuation depth h and for the deeper habitats r was calculated at depth h:

$$\int_0^h r^2 \approx c_1 S \int_0^h e^{-kz} \, dz$$
Eq. 3.3

$$r^2 \approx c_1 S (e^{-kh} - 1)/k$$
Eq. 3.4

Visual range was integrated over the first attenuation depth because this approximates the vertical habitat of tunas and because depth is not explicitly resolved in the foraging model (Chapter 4), which would increase the dimensionality beyond computational limits. In models where depth selection is the focus of study, visual range is calculated for each available depth level and habitat choice is made accordingly (e.g. Rosland & Giske 1994, 1997). The peak wavelength for the spectral sensitivity of yellowfin tuna is 490 nm (Kawamura et al. 1981); the diffuse attenuation coefficient at 490 nm (k_{490}) is therefore used here. This is directly measurable from space with the SeaWiFS ocean colour sensor (Chapter 1, Fig. 1.7). In the foraging model (Kirby et al. 2000, Chapter 4) the magnitude of the parameter c_1 was adjusted around $O(10^{-3})$ so that visual range scaled between 1 and 30 m, depending on k_{490} and time of day (i.e. surface solar irradiance S), consistent with the acuity-based results for skipjack (bold, Table 3.2. The relationship that follows between visual range and k is illustrated in Fig. 3.2.

Fig. 3.2 Visual range r varies with diffuse attenuation coefficient k. Eq. 3.3 integrated over first attenuation depth h (i.e. depth at which irradiance is 1% of that incident at the surface) $h = \ln(1/100)/k$, $c_1 = 0.01$, $S = 1000$ μE m^{-2} s^{-1}
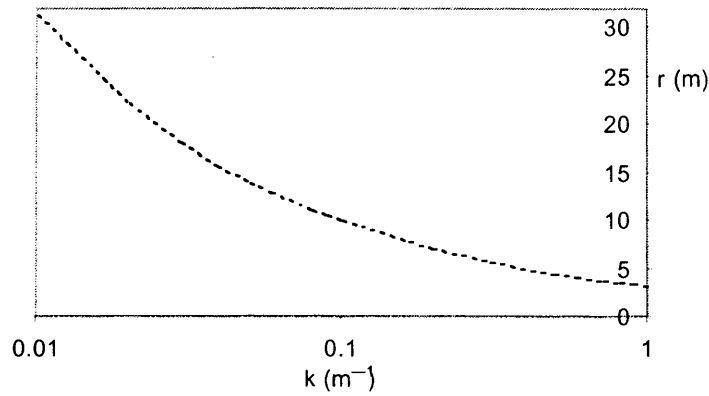
The surface irradiance experienced is not constant during the day and a correction to S by a simple sine wave was applied in order to allow for this.[1]

Fig. 3.3 Coefficient s_1 applied to peak surface solar irradiance S_{max} depending on time of day
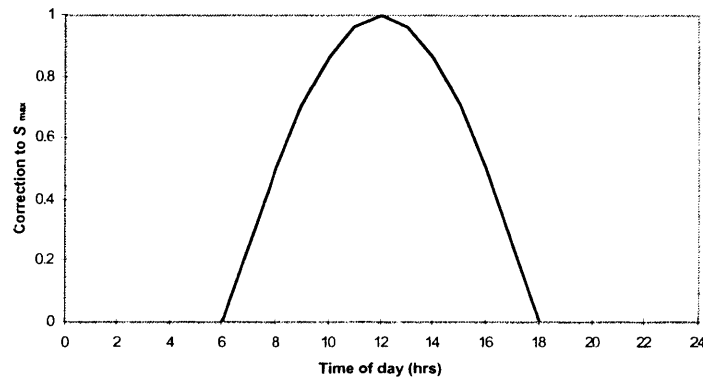
In the foraging and life history models (Chapters 4 & 5 respectively), stochastic foraging is represented by a Poisson process, where the probability p of finding food during any time stepis calculated from the deterministic encounter rate, E between the tuna and its prey:

$$p = 1 - \exp(-Et),$$
<div align="right">Eq. 3.5</div>

for:

$$E = 0.5 \ (\pi r^2 v N)$$
<div align="right">Eq. 3.6</div>

This representation has often been used in foraging models (e.g. Gerritsen & Strickler 1977, Breck 1993, Rosland & Giske 1994, 1997). The factor 0.5 in Eq. 3.6 applies to predators that are prospecting half a circular area, i.e. looking forwards and upwards.

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[1] This is only strictly valid at the equator. For other latitudes see Eqs 2 & 3 of Rosland & Giske (1994)

Encounter rate therefore depends on swimming speed, prey concentration and visual range, which is itself time-varying with S and dependent on water clarity k (Figs. 3.4 – 3.6).

Fig. 3.4 Visual range and encounter probability for tuna foraging in turbid water (k = 1)
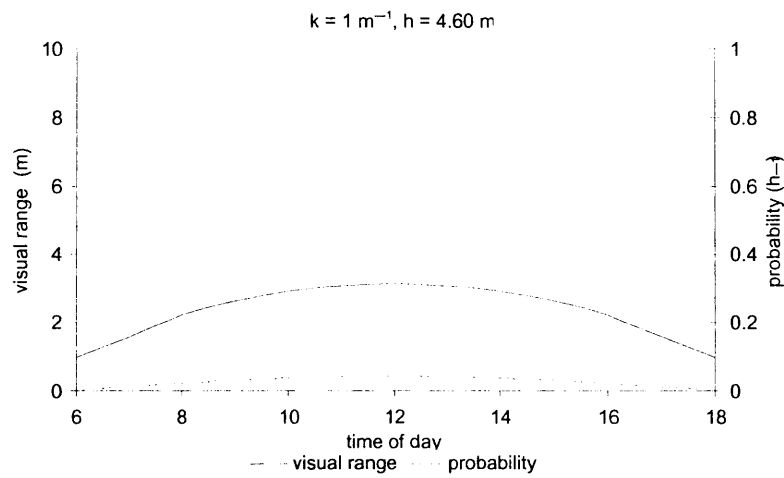
Fig. 3.5 Visual range and encounter probability for tuna foraging in clearer water (k = 0.1)
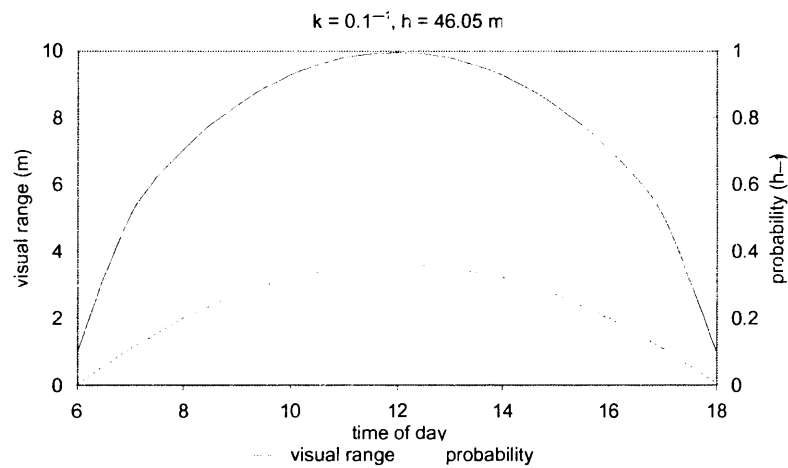
Fig. 3.6 Visual range and encounter probability for tuna foraging in very clear water (k = 0.01)
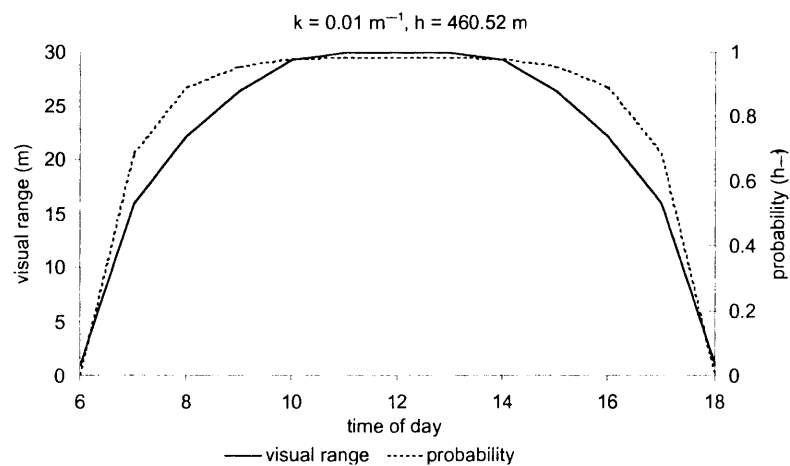
Figs 3.4–3.6 illustrate how the variation of encounter rate, as a function of visual range, determines the probability of finding food in any 1 hr time-step. For a constant food concentration and swimming speed, incident solar radiation (i.e. time of day) and water clarity (i.e. k_{490}) determine visual range, with upper and lower limits of 1 and 30 m respectively (see Table 3.2 and discussion on p. 56). In turbid water the probability of finding food at any time of day is near-zero (Fig. 3.4); in clear waters it is near-unity. Encounter rate may be increased by faster swimming, but this has consequent energy costs (see 3.3.3).

3.2.2. Olfaction

Although vision provides greater search volume and offers more precise orientation to prey than other sensory systems, information about distant objects must still be sensed by other means. Fish can sample a large area quickly, and can actively intercept an odour plume in which eddies and filaments present a dynamic stimulus pattern that may contain information about distance and direction of the source (Atema 1985). There have been comparatively few studies on olfaction in tunas (Atema et al. 1980, Williams et al. 1992). These studies went a good way towards answering the standard questions posed, i.e. what are the agents responsible for prey detection, what is the threshold concentration detectable by the predator, does the predator have any obvious preferences for different prey odours or show any signs of acclimation to an odour field? Another question that is seemingly obvious to ask when considering the role of olfaction in ecological interactions is: what is the range at which a hungry predator can detect a potential meal? With smaller fish, this question can be answered by direct measurement of range and response under controlled conditions. For larger animals such as tunas, solution to the questions asked above may still yield an answer to the question of range, but only after further mathematical treatment. Fortunately, the question is analogous to many others concerning dilution, diffusion and transport of tracers in fluid systems. Here I have defined and described some simulations based on the laboratory experiments noted above (Atema et al. 1980) and obtain length-scales for prey detection by olfaction in the open ocean.

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3.2.2.1. Experimental work

The experimental work that these simulations are based on was carried out by Atema et al. (1980) at the Kewalo laboratory of the US National Marine Fisheries Service, Hawaii. The researchers tested the behavioural responses of captive Yellowfin tuna to the odour of inshore anchovy *Stolephorus purpureus*, a very effective live bait and close relative of the tuna's most common Hawaiian open ocean prey, the 'offshore nehu' *S. buccaneeri*. In responding to a strong food odour the tuna displayed a predictable behavioural repertoire that was used as the standard for evaluating their responses to test stimuli.

3.2.2.2. Modelling dispersion in the ocean

The ocean is an aqueous solution of chemical compounds that is also highly energetic. Horizontal stirring and vertical mixing are brought about by fluxes of heat and momentum and the energy cascades from basin through to viscous length scales (Mann & Lazier 1993). Across distances greater than a few mm, turbulent eddies mix water far more effectively than does molecular motion (Okubo 1980). It is often assumed that the flux of a constituent C is dependent on the gradient of C and a turbulent diffusion constant, termed the eddy viscosity or eddy diffusivity K. We therefore obtain an analogue to Fick's law, where in 1 dimension:

$$\frac{\partial C}{\partial t} = K_x \frac{\partial^2 C}{\partial x^2}$$

Eq. 3.7

The values of K vary greatly throughout the ocean. In the deep ocean, horizontal eddy diffusivity is orders of magnitude greater than vertical diffusivity, and the diffusion of a tracer, such as a pheromone, may be considered in planar geometry (Jumper & Baird 1991). In the surface mixed layer, eddy diffusion is high in all directions and so it is better to model diffusion in both horizontal and vertical dimensions, or to assume a vertically mixed surface layer. The addition of terms in extra dimensions and solving for C, enables one to calculate the 3-dimensional spreading from a point source of a discrete mass P of conservative tracer:

$$C(x,y,z,t) = \frac{P}{(4\pi t)^{3/2}\sqrt{K_x K_y K_z}} \cdot \exp\left\{-\left(\frac{x^2}{4K_x t}\right)-\left(\frac{y^2}{4K_y t}\right)-\left(\frac{z^2}{4K_z t}\right)\right\}$$

Eq. 3.8

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Atema et al. (1980) released 20 ml of 0.1 µg.ml^{-1} Tryptophan solution; therefore $P = 2$ µg.

The threshold of detection C was $O(10^{-6}$ µg ml$^{-1})$. The detection front profile for the

dispersion of this threshold concentration over time is shown in Fig. 3.7.
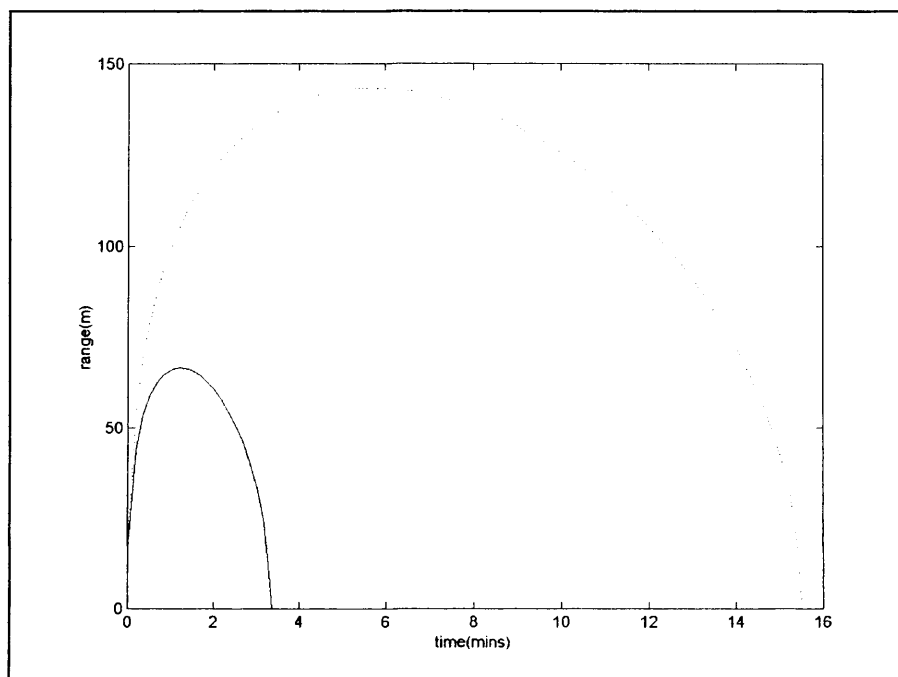
Fig. 3.7 Detection front profiles (i.e. horizontal range from source) for 3-dimensional turbulent diffusion of a point source emission of Tryptophan. Solid line, 10^{-5} µg ml^{-1} contour; dotted line, 10^{-6} µg ml^{-1} contour

This representation is only valid for the case of a point source that is discharging

discrete quantities of a tracer and is stationary with respect to the fluid. This is acceptable for

pheromone release in deep-sea fish (Jumper & Baird 1991) but not for predator-prey

interactions, where the odour of a school of forage fish is unlikely to be emitted discretely,

even if this were the case for individual fish. Furthermore, the definition of micronekton, the

size class of organisms that includes tuna prey, is that they are capable of swimming speeds

greater than the velocity of the surrounding fluid. They may therefore sustain their position in

the presence of a current. In order to determine an extreme range of prey detection by

olfaction we should therefore use equations that describe a continuous source that is

stationary with respect to the surrounding fluid.

Two different representations of the problem were considered. Both assume a steady

state regime (i.e. $t = x\, u^{-1}$) and a vertically mixed layer, with the odour diffusing as a Gaussian

distribution in the y direction (cross-stream) while being advected in the x direction (along-stream). The first case, for diffusion of a continuous point source Q g s^{-1} in a current u m s^{-1}, the concentration at any point $C(x,y)$ is given by:

$$C(x,y) = \frac{Q/h}{\sqrt{4\pi K_y x u}} \cdot \exp\left\{-\frac{y^2 u}{4 K_y x}\right\}$$

Eq. 3.9

The second model incorporates an effective strain rate, a property of fluid flow that acts to limit cross-stream diffusion and stretch a tracer along-stream (Haidvogel & Keffer 1984, Ledwell et al. 1993, 1998, Schneider 1994, Abraham et al. 2000). The solution with strain has not often been used in such studies, largely because of the absence of measurements for the effective strain rate. Recent work has provided measurements of surface strain rate (Abraham et al. 2000), that compare well with theoretical values (Haidvogel et al. 1984) and with those derived from tracer release experiments on the ocean interior (Ledwell et al. 1993, 1998). An exact analytical solution for diffusion with strain was derived (E.R. Abraham pers. comm.) and applied here. For diffusion with an effective strain rate $\gamma = 5 \times 10^{-7}$ s^{-1} the Gaussian solution is:

$$C(x,y) = \frac{Q e^{-\gamma x/u}}{2\pi\sigma h u} \cdot \exp\left\{-\frac{y}{2\sigma^2}^2\right\}$$

Eq. 3.10

where

$$\sigma^2 = \left(K_y/\gamma\right) - \left(K_y/\gamma\right) \cdot \exp\left\{\frac{-2\gamma x}{u}\right\}$$

Eq. 3.11

The same values for horizontal diffusivity K_y (10 m^2 s^{-1}), current velocity u (0.1 m s^{-1}) and mixed layer depth h (200 m) were used in both cases.

3.2.2.3. Results

Plots for turbulent diffusion and strain of a vertically mixed odour plume are given in Fig 3.8. Simulations are for a continuous emission of Tryptophan, with threshold concentrations of $O(10^{-6}$ µg ml$^{-1})$ as determined by Atema et al. (1980).

Fig 3.8 (a) horizontal spreading of 10^{-5} µg ml^{-1} contour; (b) horizontal spreading of 10^{-6} µg ml^{-1} contour. Dotted lines for diffusion, solid lines for diffusion with strain. Odour emitted at 1 g s^{-1}, vertically mixed to 200 m. Effective strain rate, 5×10^{-7} s^{-1}; horizontal diffusivity, 10 m^2 s^{-1}

(a)
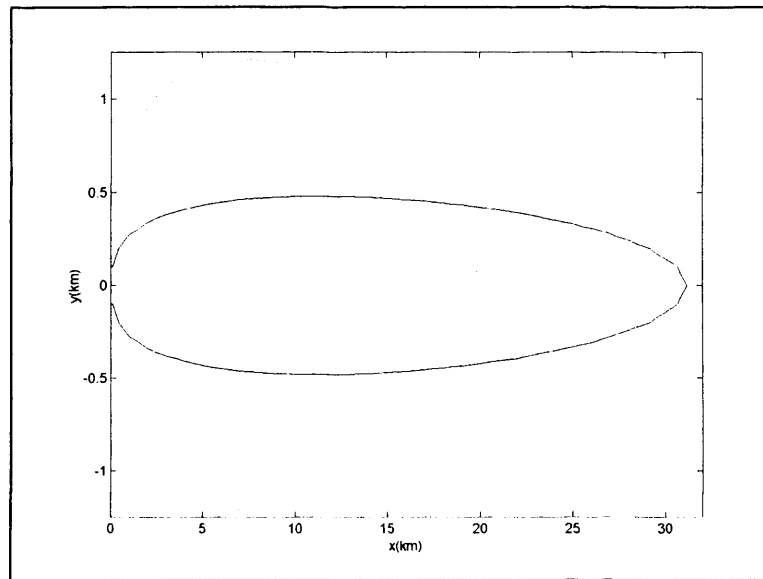
(b)
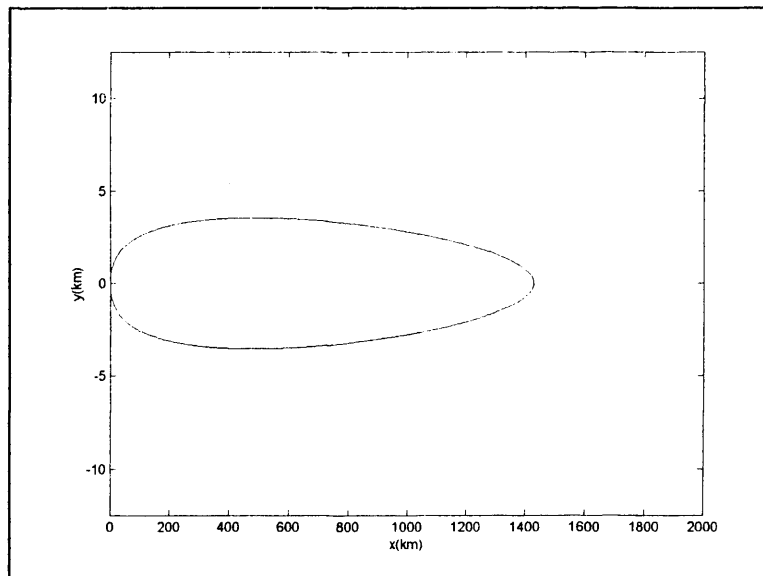
3.2.2.4. Discussion

The various representations of odour dilution and dispersion are all idealised, and mixing processes in the surface ocean are complex. Allowing for disruption of the odour plume due to finer scale turbulence, represented here only through the eddy diffusivities, the detectable range for olfaction may well be less than that predicted. Uncertainty in the results reported previously, particularly with regard to elution rates of amino acids from prey fish and also with regard to the threshold concentration for amino acid detection, carries through to uncertainty in the reaction distances calculated. The lower limit suggested as the detection threshold (10^{-6} µg ml^{-1}) propagates for $O(100$ km) from the source and in reality would probably blend into background concentrations. Even if it were detectable, to embark on a search based on chemical cues over this distance would probably be futile, given that prey is mobile and that the ocean is much more dynamic than represented here. The dilution of the upper limit suggested (10^{-5} µg ml^{-1}) is much less diffuse, and the maximum length scale that is predicted here is ~30 km. Tuna may well be able to navigate towards a signal over this distance. Swimming cross-stream when searching for the odour and up-stream in the presence of the odour is then an efficient way to locate the prey source (G Huse & R Vabo unpubl.).

Horizontal diffusion of tracers in the presence of strain is limited to a scale of ~5 km, determined by $\sqrt{K_y/\gamma}$ even if the tracer is non-conservative, e.g. phytoplankton (Martin 2000). The width of filaments in the model regime here ($K = 10$ m^2 s^{-1}, $\gamma = 5 \times 10^{-7}$ s^{-1}) is 4.5 km.

The width of the detectable odour plume depends on the sensitivity of the predator and is predicted here to be ~1 km for the 10^{-5} µg ml^{-1} contour (Fig. 3.7a). In the vertical dimension odours may not be well-mixed, due to stratification of the water column. In such circumstances an odour trail may be longer and more concentrated but harder to initially detect. The 'dive & glide' behaviour observed in tunas (Weihs 1973, Carey & Olson 1982, Holland et al. 1990, Block et al. 1997) whereby a rapid powered ascent is followed by a

slow, lift-based glide, may not only be a way of conserving energy but may also represent an efficient search strategy, permitting sampling of different depth strata for odour trails.

3.2.3. Summary

Reaction distances for prey detection by vision and olfaction have been calculated using 2 different analytical models in each case. The purpose of this exercise was to identify horizontal limits to the efficiency of these sensory systems. Conclusions are confounded by the lack of published information on visual capacity and other important properties of tuna eyes and the inherent contrast of different prey types (cf Aksness & Giske 1993, Aksnes & Utne 1997), elution rates of detectable odours (i.e. amino acids) from forage fish and the imprecise determination of the sensitivity threshold for prey detection by olfaction. Nonetheless, it is possible to use 'sensible' estimates of these parameters in the analytical models available in order to estimate maximum values for each case. I conclude that tunas are able to detect their prey by vision at a range of 1 to 30 m, depending on turbidity and prey (shoal) size, and by olfaction at a range of up to 20–30 km, depending on prey concentration, currents and the degree of stratification. These estimates are used to constrain predator-prey encounter rates in the foraging model (Chapter 4) and life-history model (Chapter 5) that follow.

3.3. ACTIVE METABOLIC RATE

Tunas have metabolic rates up to 5 times higher than those of other comparable teleosts (e.g. salmon and trout, Brett & Glas 1973; Gooding et al. 1981, Brill 1979, 1987, Dewar & Graham 1994, Brill 1996). The active metabolic rate is the sum of standard metabolic rate, specific dynamic action and energy cost due to locomotion, and experiments have been carried out to determine the relative contributions of these components to total energy cost.

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3.3.1. Standard metabolic rate

Standard metabolic rate (SMR) is the metabolic rate of an animal completely at rest at a temperature to which it has adapted. The SMRs of Skipjack and Yellowfin tuna have been determined (Brill 1979, 1987 respectively and for both species by Dewar & Graham 1994) at their preferred temperature of 25°C, and the effects of body size and acute temperature change were studied. Allometric equations relating SMR to body mass were derived from experimental data, with the form: $SMR = aM^b$, where M is body mass and both a and b are fitted parameters. The curves that follow from this relationship, with parameters fitted for Skipjack (a = 412 ± 27.1, b = 0.563 ± 0.07, Brill 1987) and Yellowfin (a = 286.8 ± 26.9, b = 0.573 ± 0.116, Brill 1989), are shown in Fig. 3.9, with SMR converted from mg O_2 h^{-1} to kJ h^{-1} (1 mg O_2 = 14.054 J). The effect of body mass on SMR is not significantly different between the 2 tuna species but the exponents in the allometric equation are lower than for other teleosts, indicating that weight-specific SMR for tunas decreases more rapidly as body size increases (Brill 1987).

Fig. 3.9 SMR by body mass for Skipjack and Yellowfin (Brill 1987, 1989)
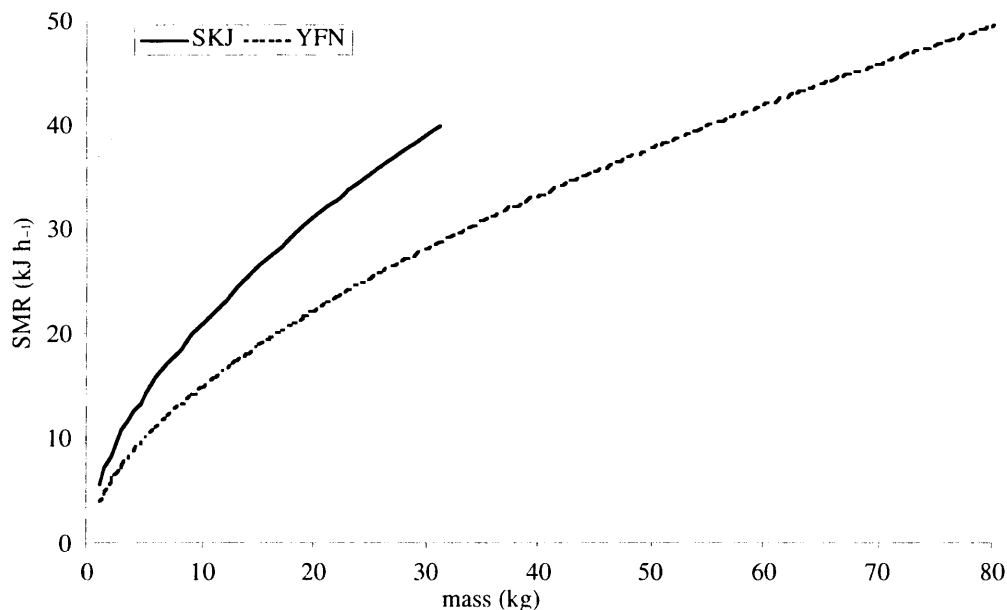
3.3.2. Specific dynamic action

'Specific dynamic action' is the energetic cost of converting food into useable energy and is a direct function of stomach fullness; there is a sharp increase in metabolic rate shortly after ingestion of a meal, peaking at ~2 times the pre-feeding rate within a few hours and falling off to the pre-feeding level over the time that it takes for the stomach to empty (Jobling 1994). This has been modelled using a step-function with 2 linear relationships: over the first 2 h following ingestion SDA increases from zero (i.e. no food is being converted) to a value equivalent to the SMR; metabolic energy costs therefore double and then decrease to the normal SMR over the next 8 h (Fig. 3.10).

3.3.3. Cost of locomotion

The energy cost due to locomotion E_L is a function of body length L, swimming speed cubed v^3 and drag C_d (Sharp & Francis 1976, after Streeter 1962):

$$E_L = 2.59 \times 10^{-5} \ L^2 \ v^3 \ C_d \qquad (\text{mg O}_2 \ \text{hr}^{-1}) \qquad \qquad \text{Eq. 3.12}$$

The drag coefficient C_d is also a function of body length and velocity (Gerritsen 1984, after Webb 1975) and can be approximated as:

$$C_d = 0.55 \ L^{-1/2} v^{-1/2} \qquad \qquad \text{Eq. 3.13}$$

which, when substituted into Eq. 3.12 and converted to Joules (1 mg O_2 = 14.054 Joules) gives:

$$E_L = 2.002 \times 10^{-4} \ L^{1.5} \ v^{2.5} \qquad \qquad \text{Eq. 3.14}$$

The energy cost of foraging is compared with the encounter rate for various velocities in Fig.3.11. This illustrates the trade-offs that operate, as encounter rate is a linear function of v (Eq. 3.5) and energy cost varies with $v^{2.5}$ (Eq. 3.14).

Fig. 3.10 Variation of metabolic rate with stomach fullness (i.e. standard metabolic rate plus specific dynamic action)
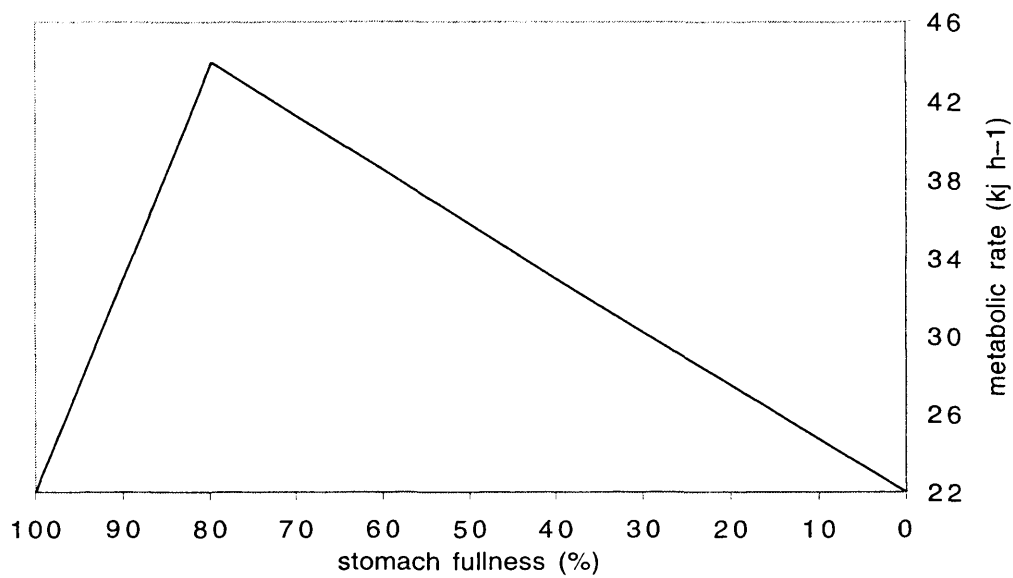
Fig. 3.11 Trade-off between energy cost and encounter rate for varying swimming speed. In the foraging model swimming speed is included in the optimisation criterion and is not predicted to exceed 4 m.s^{-1}
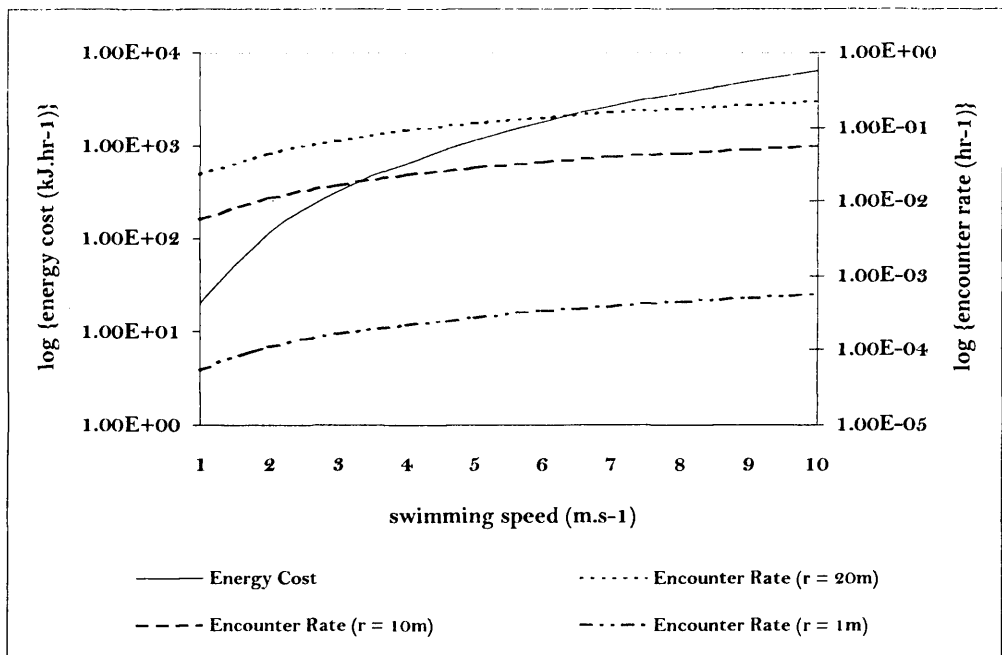
3.4. ENERGY ABSORPTION & GASTRIC EVACUATION

Experimental work has shown that when food is available, tuna will feed until satiated in less than 1 h (Olson & Boggs 1986). Tunas also have exceptionally high digestion rates (Magnuson 1969, Olson & Boggs 1986, Brill 1987, 1996) evacuating their stomachs within 10–14 h after ingestion (Magnuson 1969, Olson & Boggs 1986). Other piscivores of similar body length require 4 to 5 times longer than Skipjack to evacuate a meal (Magnuson 1969). This facility is advantageous for species that must be able to exploit potentially short-lived aggregations of food whenever they are encountered. Rapid energy absorption may then occur for low energy prey items (Olson & Boggs 1986, Andersen 1999) and in warmer waters where metabolic rate and therefore absorption efficiency is higher (Jobling 1994).

The foraging model (Kirby et al. 2000, Chapter 4) allows the stomach to be refilled to capacity at each prey encounter. Rather than fixing a linear or logarithmic rate of gastric evacuation, it is instead determined by the rate of energy absorption from the stomach (Fig. 3.12). The amount of energy in the stomach is determined by the relative amounts of the possible prey types and their respective energy densities. The stomach is capable of absorbing a fixed amount of energy in each time step. The amount of energy actually absorbed is determined by the absorption coefficient q_2, which varies directly with metabolic rate (SMR + SDA). Previous work (Kitchell et al. 1978) found that absorption efficiency (i.e. energy absorbed from energy ingested) was 90% for a diet of fish and 80% for a diet of invertebrates. Here 100% absorption is assumed, an approximation that allows the energy absorbed per time step to determine the rate of gastric evacuation (Figs. 3.12 & 3.12, see Chapter 4 for more details). While the slopes for gastric evacuation are the same, the time taken to empty the stomach is less for lower energy food (cf citations above). This implies that energy absorption is a continuous process but gastric evacuation is not. The small accumulation of waste then precedes a pulse of evacuation.

Fig. 3.12 Energy absorption from the stomach and subsequent gastric evacuation. Starting with a full stomach (X_o) with maximum stomach energy (Y_{max}), a proportion ($q_2 Y_{max}$) is absorbed during the first time step. An amount of stomach contents is then evacuated, such that the energy density of the stomach contents (Y/X) is unchanged. The amount of energy absorbed in each time step varies because the absorption coefficient (q_2) depends on metabolic rate. This doubles 2 h after feeding and then decreases to the pre-feeding rate
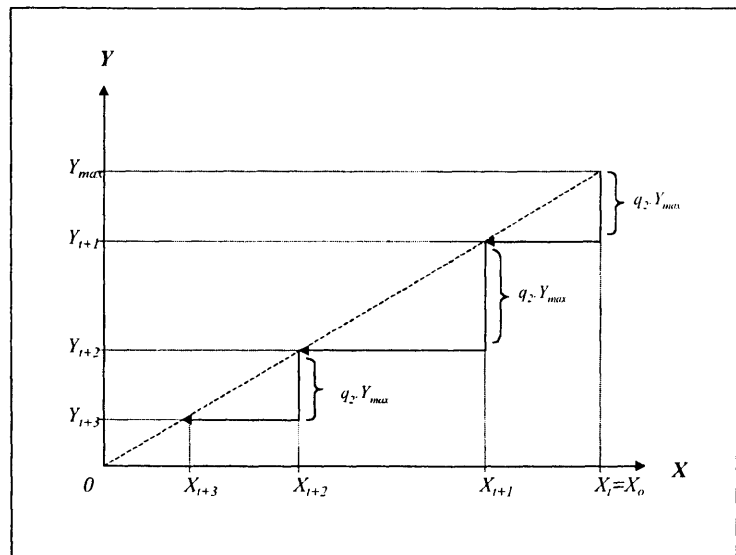
Fig. 3.13 Rates of energy absorption and gastric evacuation for different prey energy densities at different temperatures. Note the rapid evacuation of stomach contents when prey quality is poor and the slower absorption and evacuation rates at lower temperatures. Energy absorption is a continuous process; gastric evacuation is pulsed
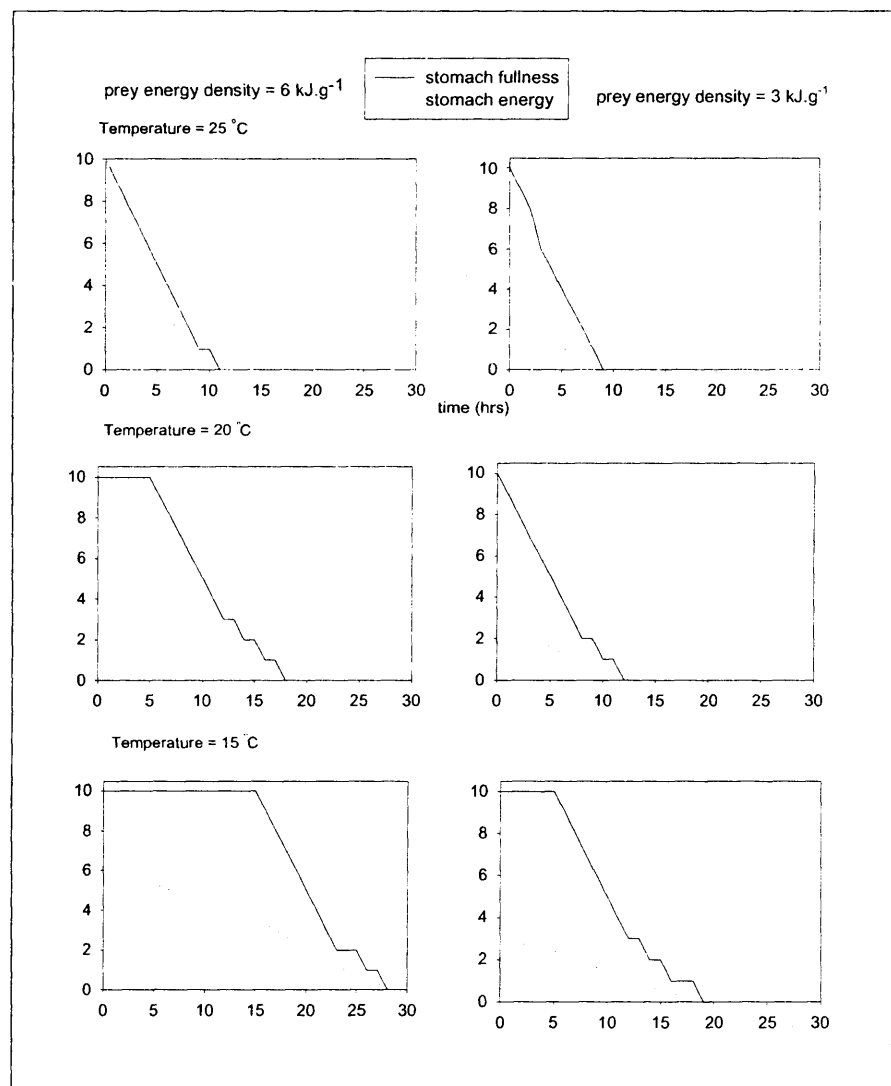
3.5. THERMAL STRESS

When experiencing acute temperature changes, SMR responds with a $Q_{10} \approx 2$, i.e. it doubles (halves) for every 10°C increase (decrease) in ambient temperature (Brill 1987). This is similar to values reported for other teleosts, despite the mechanisms of heat conservation available to tunas (see Chapter 1). This has been a puzzle until recent experiments showed that water temperature has a direct effect on heart rate (Brill 1997, Brill et al. 1998). The heart is effectively 'outside' the heat-exchange system (Brill et al. 1994b) and the temperature of the heart will therefore immediately relect changes in ambient temperature. Experiments on Yellowfin have shown that an acute reduction in temperature results in an immediate decrease in heart rate ($Q_{10} = 2.37$, Korsmeyer et al. 1997a; Brill 1997, Brill et al. 1998). Unlike most teleosts, tunas depend more on increased heart rate than increased stroke volume when elevated levels of cardiac output are needed (Farrel 1991, Farrel et al. 1992, Korsmeyer et al. 1997a,b) yet they have no apparent ability to counteract the decreased heart rate and cardiac output that results from acute reduction in temperature (Brill 1997, Brill et al. 1998). This means that although they might be able to maintain oxygen delivery at low swimming speeds they would not be able to sustain higher swimming speeds at low temperatures. Such temperature limitation may be fatal. Captive skipjack could not survive more than a few hours in waters only 5°C outside the optimal temperature range, i.e. 15°C and 35°C (Dizon et al. 1977, Barkley et al. 1978). The cause of death under thermal stress is most likely due to falling heart rate and cardiac output rather than effects on muscle temperature and efficiency and energy losses (Brill et al. 1998). Bigeye tunas are able to tolerate colder waters for longer periods of time than other tropical tunas, which has been attributed to rapid increase in blood temperature when in warmer waters (Holland et al. 1992, Dewar et al. 1994) and also to the unique properties of Bigeye blood itself (Brill 1997), which has a significantly higher O_2 affinity than the blood of other tunas (Lowe et al. 2000).

In the foraging model (Kirby et al. 2000, Chapter 4) this subject is treated separately from the other bioenergetic state variables. A state variable Q is incremented with time spent in waters outside the preferred temperature range and decreased when the fish returns to warmer waters. The rates of increment (Table 3.3) are set such that Q reaches the lethal maximum in the time given by the experiments referred to above (Dizon et al. 1977, Barkley et al. 1978). The rates of increment and recovery may be non-linear and variable (e.g. Holland et al. 1992). The recovery rate for Q is therefore greater than the rate of increment by a factor of 10 (Table 3.3). A direct effect of Q on overall fitness was also included (Chapter 4).

Table 3.3 Increment/decrement of state variable Q by coefficient q_3 (see Eq. 4.6) that results after 1 h at given temperatures. Tuna dies ($Q = 5$) after 5 h in water 5°C colder than minimum value of preferred temperature range. Time permitted in colder waters based on these rates are given. Recovery from thermal stress is rapid i.e. q_3 is large and negative in warm waters

Water Temperature (°C)	Hourly increment/decrement of thermal stress, Q (i.e. q_3)	Time until death (h)
15	1	5
16	0.64	8
17	0.36	14
18	0.16	31
19	0.04	125
20	0	-
21	-2	-
22	-4	-
23	-5	-
24	-5	-
25	-5	-

A summary of characteristics used to define a model tuna in the behavioural and life history models developed later on (Chapters 4 & 5) is given in Table 3.4.

Table 3.4 Characteristics of the artificial tuna (ARTU) used in the optimal foraging model (Chapter 4) compared to published data. Omissions occur where no published information is available. ARTU is derived to have characteristics similar to those measured for Skipjack & Yellowfin

Property	Units	ARTU	Skipjack	Yellowfin	Albacore	Bigeye	S. Bluefin
Maximum length[2]	cm	100	110	280	130	250	225
Maximum weight[1]	kg	20	35	200	45	210	200
Stomach capacity / body mass	%	5	-	5.46–5.97[3]	-	-	-
Maximum somatic energy density	kJ.g^{-1}	6	6.2[4]	6.0[3]	-	-	-
Minimum somatic energy density	kJ.g^{-1}	3	3.1[3]	3.7[3]	-	-	-
Maximum swimming speed	lengths.s^{-1}	10	14.4[5]	10[4]	-	-	-
Minimum swimming speed	lengths.s^{-1}	1	1.5[6]	1.3[5]	-	1.1[5]	-
Preferred (Optimal) temperatures	°C	20–30	17 (20–29) 30 [7]	18 (24–30) 31[6]	11 (16–19) 25 [6]	11 (23–28) 28 [6]	10 (13–15) 28 [6]
Standard Metabolic Rate for 20kg fish	kJ.hr^{-1}	22	30[8]	22[7]	15[9]	-	-
Lethal limits of temperature (Time @ Temperature)	hrs, °C	5. 15	5, 15[10]	-	-	-	-
Q$_{10}$ for temperature effect on SMR	-	2	2.2[7]	2.2[7]	-	-	-
Visual range	m	1–30	-	-	-	-	-

[2] Collette & Nauen 1983
[3] Olson & Boggs 1986
[4] Boggs & Kitchell 1991
[5] Yeun 1966
[6] Magnuson 1973
[7] Freon & Misund 1999
[8] Brill 1987
[9] Brill unpubl. in Graham & Laurs, 1982.
[10] Dizon et al. 1977, Barkley et al. 1978

CHAPTER 4

AN OPTIMAL FORAGING MODEL

FOR TUNAS AT OCEAN FRONTS

CONTENTS

4.1. SUMMARY

In this chapter I present a model that simulates the foraging behaviour of tunas in the vicinity of ocean fronts. Stochastic dynamic programming is used to determine optimal habitat choice and swimming speed in relation to environmental variables (water temperature and clarity) and prey characteristics (abundance and energy density). By incorporating sub-models for obligate physiological processes (gastric evacuation, standard and active metabolic costs) and sensory systems (visual feeding efficiency) described in Chapter 3, many of the factors that have long been argued to explain the aggregation of tunas at ocean fronts are integrated into a single fitness-based model. The modelling technique describes fitness landscapes for all combinations of states and makes explicit, testable predictions about time- and state-dependent behaviour. Enhanced levels of searching activity when hungry and towards the end of the day are an important feature of the optimal behaviour predicted. The model is particularly representative of the behaviour of tropical tunas and young temperate tunas that are often observed to aggregate near fronts. For adult temperate tunas plus the tropical Bigeye tuna, for which extended vertical migrations are a significant and as yet unexplained component of behaviour, the model is able to reproduce observed behaviour by adopting the lower optimal temperature and standard metabolic rate of Albacore. The model is the first detailed attempt to predict tuna behaviour from physiology and environment. It cannot explain why physiological differences exist between and within species, but it does show how differences in susceptibility to thermal stress will permit different behaviour.

4.2. INTRODUCTION

Ocean fronts are broadly understood to mark the boundary between 2 different water types (Fig. 1.7) and are therefore usually manifested as a region of strong horizontal gradients in temperature, salinity, and chlorophyll, and concentration of zooplankton and micronekton. Blackburn (1965) noted that fronts are very important in the ecology of tunas and other macronekton, but that the reasons for this were rather poorly understood. Even now there are no datasets that allow a definitive assessment of trophic interactions at fronts, particularly with regard to the behaviour of tunas (Olson et al. 1994). Whilst it is generally accepted that tunas aggregate at fronts, presumably to feed (Laurs et al. 1984, Fielder & Bernard 1987) field observations do not show for all cases that tunas and their prey are more abundant in or at fronts than in adjacent waters (Sund et al. 1981, Power & May 1991). The reasons offered as to why such association occurs, include the following (listed in Laurs et al. 1984): confinement to a physiologically optimum temperature range (Thompson 1917, Sund et al. 1981), utilisation of frontal gradients for thermoregulation (Neill 1976), limitation of visual hunting efficiency due to the effects of water clarity (Magnuson 1963, Murphy 1959), and the availability of appropriate food (Pinkas et al. 1971). Other authors have subsequently referred to Laurs et al. (1984) as defining the behaviour of tunas in relation to ocean fronts, using statements such as, 'tunas aggregate at temperature fronts in order to feed (Laurs et al. 1984)'. As noted in Chapter 1, the confusion between establishing associations and proving cause and effect constitutes 'the error of pseudo-explanation' (Loehle 1987). While Laurs et al. (1984) discussed the role of the environmental variables listed above, they did not investigate their relative importance nor establish any causal links between them and the distribution of tunas. This model was developed as a tool that might aid such investigation and help to guide and interpret future observations, thus providing a deeper level of understanding of the association between tunas and ocean fronts.

4.2.1. Context & objectives

Tuna behaviour is investigated in the context of optimal foraging theory, where the individual is seeking to maximise energy return from foraging activity in a heterogeneous environment (MacArthur & Pianka 1966, Emlen 1966, Stephens & Krebs 1986, Schoener 1987). The objective of the exercise was to develop a model system for a generic tuna that would predict optimal foraging behaviour in relation to the biophysical environment. Environmental cues and functional responses are linked through the mechanisms that operate, and obligate physiological processes are represented at an appropriate level of detail. Through this work I wished to suggest a methodology for integrating tuna physiological and behavioural ecology within a quantitative framework, with a sound theoretical basis, and ultimately a predictive capability. The model was developed with two essential questions in mind:

1. Is the observed aggregation of tunas at ocean fronts predicted by any single property or combination of properties of the fish themselves or of their environment?

2. Are the observed inter- and intra-specific variations in behaviour also predictable?

By investigating these questions I hoped to provide explanations for tuna behaviour that went beyond the present level of understanding, placing observations in a theoretical context and identifying requirements for further observational and experimental study.

4.3. THE MODEL

4.3.1. Environment

The ocean environment is represented in 2-dimensional space and time, with two vertical layers and two surface water masses with a frontal zone between them (Fig. 4.1). The fish may therefore inhabit any 1 of 7 possible habitats at any given time. As the time-step used in the model is 1 h, the fish is allowed to move between all possible habitats without constraint. The properties of these habitats (Table 4.1) are used as inputs to the model.

Figure 4.1 Schematic representation of habitat choice for tunas in the vicinity of a coastal upwelling front

| 6 | | 5 | 4 | 3 | | 2 |

FRONTAL ZONE

coastal surface

oceanic surface

1

7

oceanic deep

coastal deep
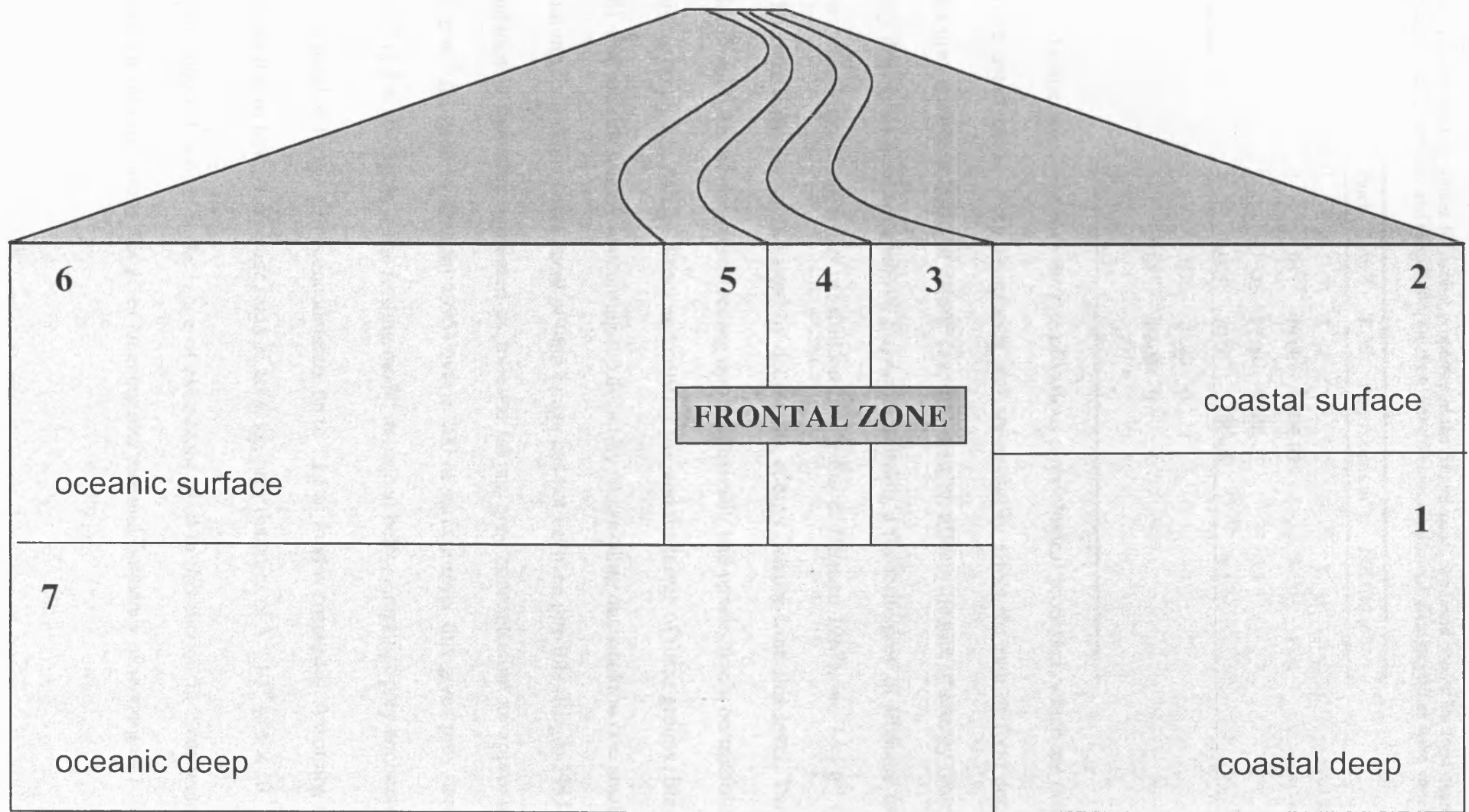
Table 4.1 Some realistic values for habitat properties at the frontal zone: estimated values for food quantity (N) and quality (PED), turbidity and temperature are used. For different simulations these quantities were varied.

Patch	k (m^{-1})	T (°C)	Prey (shoals.m^{-3})	PED (kJ.g^{-1})
1	-	-	-	-
2	0.04	18.00	0.40E-07	6
3	0.0325	19.00	0.20E-07	5.5
4	0.025	20.00	0.10E-08	5.5
5	0.0175	21.00	0	-
6	0.01	22.00	0	-
7	-	-	-	-

Temperature relates to the rate of various physiological processes, which are described in more detail below. Prey abundance and water clarity affect the rate of food encounter whilst prey quality in terms of caloric (energy) density, affects the rate of energy return. The energy density of northern anchovy *Engraulix mordax*, a favourite prey of albacore foraging at the coastal upwelling fronts off California (Fiedler & Bernard 1987), is ~7 kJ.g^{-1} (Boggs 1991). Here prey quality is varied by decreasing energy density from this level. Tunas are predominantly visual predators, feeding opportunistically and unselectively on micro-nekton, including epipelagic fish, molluscs and crustaceans, and the larvae of these groups (Blackburn 1968). For reasons largely concerning the difficulty of sampling micronekton (i.e. small, fast-swimming fish) direct assessment of tuna forage has not yet been possible (Roger 1994). Prey abundance is therefore estimated as follows: taking prey concentration as approximately 1–10 g m^{-2} (as used by Dagorn 1995) over a 200 m surface layer this gives prey density of 5 × 10^{-5} to 5 × 10^{-4} kg.m^{-3}. The feeding model described below simplifies prey encounter such that if a shoal of forage fish is encountered, up to 1 kg of food is consumed. Assuming a shoal of forage fish to have an average mass of 1000 kg, prey densities of 5 × 10^{-8} to 5 × 10^{-7} shoals m^{-3} are obtained, which is the range of abundance used in this model. In clear water with realistic swimming speeds this gives an encounter rate and frequency of feeding of 1–2 meals day^{-1}.

4.3.2. Physiology & sensory biology

The physiology of the fish is the state space of the model, described in more detail in Chapter 3 and below as the evaluation of fitness is discussd. The behavioural options optimised in the model in relation to environmental properties and state variables determine the probability of finding food. Prior knowledge of environmental properties, including food type and concentration, is implicit in the modelling technique. Olfaction might explain this — the reaction distance is then determined by visual range.

4.3.3. Evaluation of fitness

The technique used for the study is *stochastic dynamic programming* (SDP). The outputs of an SDP model are the state- and time-dependent choices that maximise some measure of fitness, and the technique is particularly appropriate to behavioural studies incorporating different components of fitness (McFarland 1977, Mangel & Clark 1988, Krebs & Davies 1991, Giske et al. 1998). The fitness criterion used here is not a true measure of Darwinian fitness but is a proxy for the general health of the fish, and therefore its reproductive ability. Issues regarding allocation of energy to somatic and gonadal growth have not been considered but the model works on the assumption that at low levels of total body energy, growth, reproduction and migration are limited.

The 'Terminal Fitness Function' (Mangel & Clark 1988) was therefore defined such that fitness F is scaled according to the level of somatic energy density above a critical level:

$$F(x,y,z,Q,H,H) = \begin{cases} \left(\dfrac{z - z_{crit}}{z_{max} - z_{crit}} \right)^{\zeta} & \text{if } z > z_{crit} \\ 0 & \text{if } z \leq z_{crit} \end{cases}$$

Eq. 4.1

where x, y, z and Q are the state variables described above, H is the time horizon and z_{max} and z_{crit} are the maximum and minimum (critical) levels of body energy. The shape of the Terminal Fitness Function can be varied by raising it to various powers ζ — higher body energy is then required to obtain high fitness — motivation for foraging is then increased (Eq. 4.1, Fig. 4.2).

By backward iteration from terminal fitness, fitness values for all combinations of

state, habitat i, and swimming speed s over time t are obtained using the 'Dynamic

Programming Equation' (Mangel & Clark 1988):

$$F(x,y,z,Q,t,H) = \begin{cases} \max_{i,s} q_4 \left[\begin{array}{l} p_1 F(x',y',z',Q',t+1,H) + \\ (1-p_1)F(x'',y'',z'',Q'',t+1,H) \end{array} \right] & \text{for } z > zcrit \\ 0 & \text{for } z \leq zcrit \end{cases}$$

Eq. 4.2

where p_1 is the probability of finding food, and the dynamics of the state variables are:

If food is encountered (with probability p_1):

$$x' = X_o$$

Eq. 4.3a

i.e. stomach is filled;

$$y' = y - q_2\, y_{max} + (X_o - X)\, \rho_E$$

Eq. 4.3b

i.e. energy is absorbed from the stomach and new energy is ingested.

If food is not encountered (with probability $1-p_1$):

$$y'' = y - q_2\, y_{max}$$

Eq. 4.4a

$$x'' = y''\, x\, y^{-1}$$

Eq. 4.4b

i.e. energy is absorbed from the stomach and the new stomach energy, y'' determines the new

stomach fullness (see Fig. 3.2), as waste (i.e. mass with negligible energy) is evacuated.

For all cases:

$$z' = z'' = z + q_2\, y_{max} - \alpha$$

Eq. 4.5

i.e. body energy is incremented by absorption from the stomach, minus total energy costs;

$$Q' = Q'' = Q + q_3$$

Eq. 4.6

i.e. thermal stress changes depending on ambient temperature (Table 3). The level of thermal

stress may then have a direct, non-linear effect on fitness through the coefficient q_4 (Fig. 4.3):

$$q_4 = (Q_{max} - Q)/Q_{max}$$

Eq. 4.7a

$$q_4 = 1 - (Q/Q_{max})^2$$

Eq. 4.7b

Fig. 4.2 The Terminal Fitness Function (linear & quadratic)
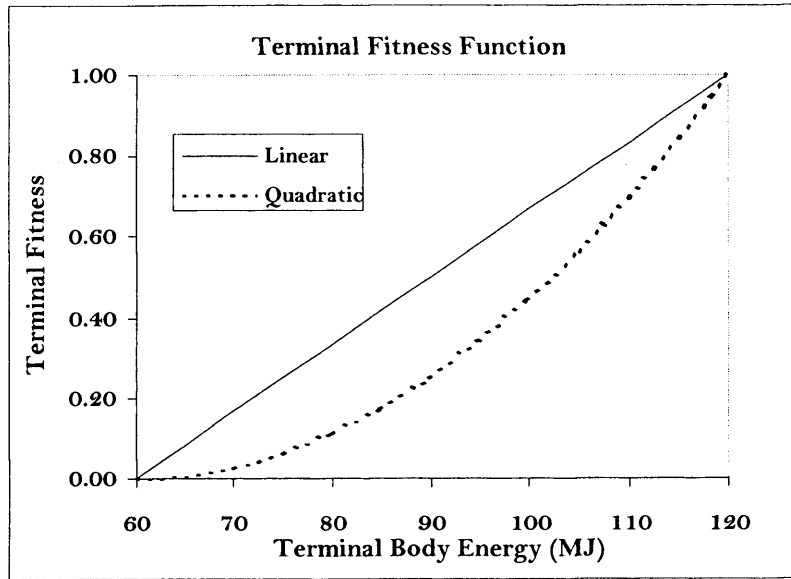
Fig. 4.3 Direct effect of thermal stress Q (linear & quadratic) through coefficient q_4
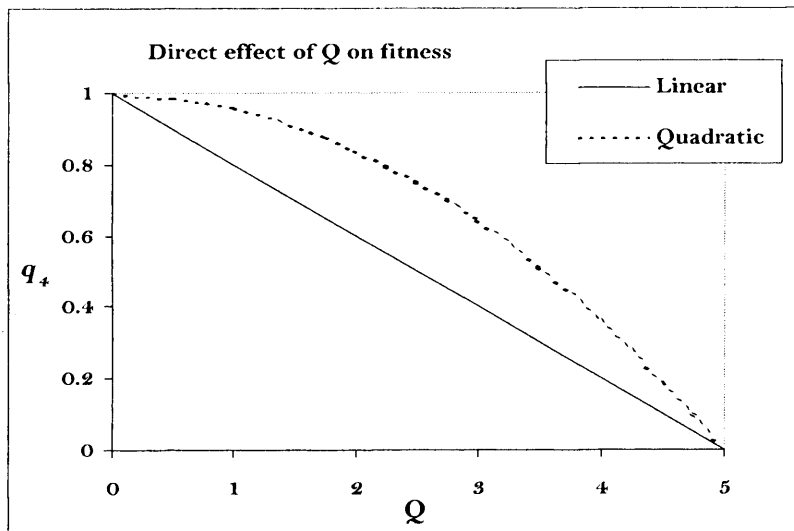
Once the fitness values for all possible solutions are calculated, the optimal solutions (i.e. optimal habitat and swimming speed for any combination of states and time) are saved. An individual based model (IBM) can then run forwards in time, simulating foraging with stochastic prey encounter; the state dynamics and behaviour may be recorded. Some results for fitness landscapes, optimal behaviour and foraging simulations are presented below.

4.4. RESULTS

4.4.1. Foraging at Fronts

4.4.1.1. Fitness landscapes

These represent the fitness values for combinations of the 4 state variables over time and are illustrated in Fig. 4.4. In Fig. 4.4a, fitness for different values of stomach fullness X over time is shown for different levels of body energy Z. Fitness decreases slightly with stomach fullness and there is a small diurnal effect, such that fitness is lower for an unfilled stomach towards the end of the day than it is for the same level of stomach fullness at the start of the day. These fitness landscapes are significantly affected by the level of body energy; if body energy is high it matters little whether or not the stomach is full. As body energy decreases, variations in stomach fullness become more important determinants of fitness. In Fig. 4.4b, fitness for different values of body energy Z over time is shown for different levels of thermal stress Q. At any time t there is significant variation in fitness as body energy is varied, and as thermal stress increases, all fitness values are reduced.

4.4.1.2. Optimal habitat choice and swimming speed

For conditions where only single properties varied between habitats, the results are simply described. For scenarios where all properties vary between habitats (Table 4.1), plots of optimal habitat and swimming speed and of foraging simulations are included. Swimming speed greater than the minimum value indicates active foraging.

Effect of temperature variations: If food quality and quantity do not vary between habitats, but temperature varies from 25°C offshore to 15°C inshore, the optimal habitat to inhabit is the one where temperature is just above the threshold for the accumulation of thermal stress. Here metabolic energy costs are lowest and no thermal stress is incurred.

Role of food quantity and quality: If there is food in only 1 habitat and all other conditions are equal, then it is optimal to be in that habitat. If there is equal abundance in all habitats but food quality varies, then the optimal habitat is the one with the most energetic food. If there is an unequal distribution of food and quality also varies, then the best place to be is an intermediate habitat which has good quality food and higher than average abundance.

Fig. 4.4 (a) Fitness for different values of stomach fullness X over time, at different levels of body energy Z; thermal stress Q is zero. There is a small diurnal effect, such that fitness is lower for an empty stomach at the end of the day than in the morning. In general fitness values are fairly constant with stomach fullness, but are significantly affected by the level of body energy. (b) Fitness for different values of body energy Z over time, at different levels of thermal stress Q; stomach fullness is 50%. There is significant variation in fitness as body energy is varied; as thermal stress increases all fitness values are much reduced

Effect of visual range and light: Swimming speed is generally faster during the day, when light intensity and therefore visual range are high. If food has not been encountered as daylight is fading, swimming speed may increase for a few hours before falling again, a prediction that follows from the fitness landscapes described above. At night, when visual range is near zero, swimming speed usually dropped to the minimum value. Diffuse attenuation coefficient k, being in the exponent of the visual feeding model, was a major determinant of foraging behaviour.
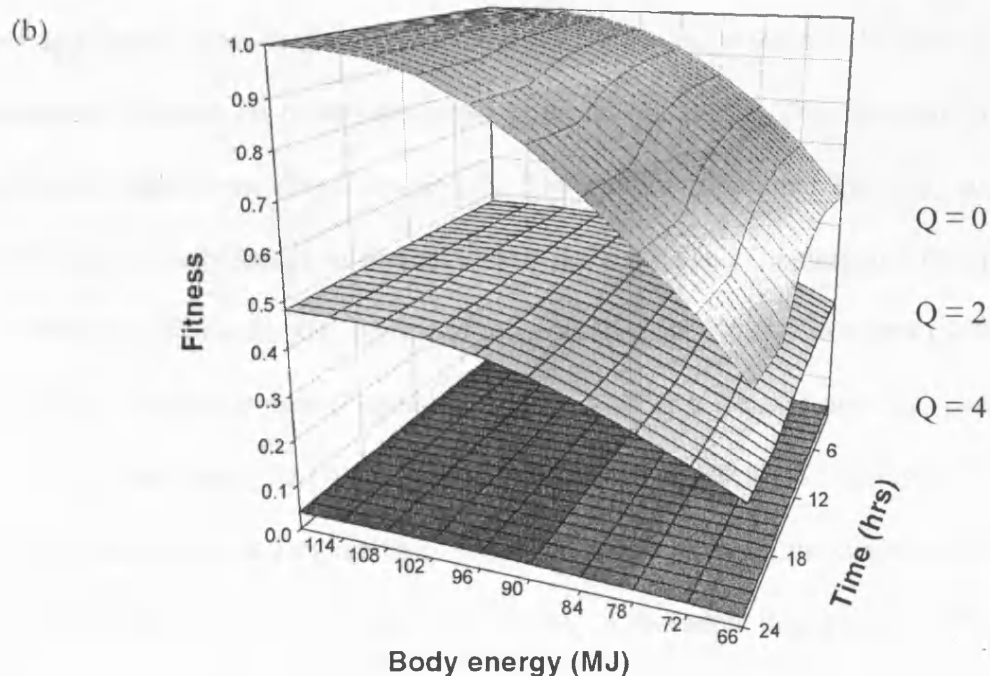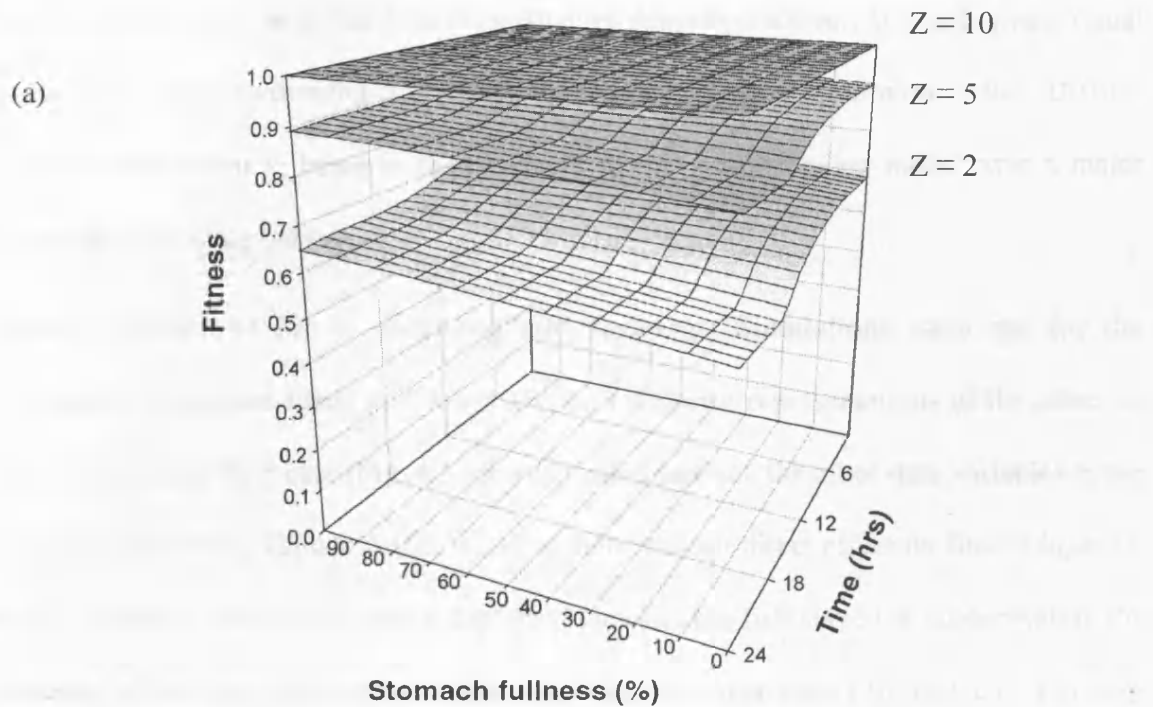
Foraging simulations for a quasi-realistic scenario: Simulations were run for the environmental properties listed in Table 4.1 with 3 different representations of the effect of thermal stress. In the first case (Fig. 4.5) Q was treated just like the other state variables in the Dynamic Programming Equation (Eq. 4.2) *i.e.* there was no direct effect on fitness ($q_4 = 1$). Active foraging occurred only during daylight hours but the fish stayed in colder waters for the majority of the time, only occasionally returning to warmer waters to reduce Q. I did not consider this original formulation to be well representative of the physiological mechanisms acting and the behaviour that resulted did not seem very realistic. I therefore incorporated a direct and linear effect of Q on fitness through Eq.16a, representing the immediate effect of temperature change on heart rate (Brill et al. 1998, 1999). This resulted in much more conservative behaviour (Figs. 4.6 & 4.7). The optimal solutions (Fig. 4.6) show that tuna should only actively forage in coastal waters if the stomach is empty and during the middle 4 h of the day (10:00–14:00); the rest of the time they should stay in warmer offshore waters, swimming at their minimum speed. Foraging is still a diurnal activity, peaking around midday, but time spent in colder waters is extremely limited (1–2 h, Fig. 4.7). Again, this behaviour did not seem very realistic. I then varied the shape of the function determining the direct effect of Q on fitness, implementing Eq. 4.7b rather than Eq. 4.7a (Fig. 4.3). This prolonged the time permitted in colder waters (Fig. 4.8 & 4.9) and behaviour is then not so conservative. Active foraging occurs from 07:00–17:00 when stomach fullness is less than 70%; if stomach fullness is below 20% between 09:00 and 15:00, the fish should also move to

the coastal waters (Fig. 4.8a,b). At night, active foraging does not occur; the warmest offshore waters (Habitat 6) are occupied if there is food ($\geq$ 20%) in the stomach, otherwise the fish should stay in Habitat 4. Within the constraints of the model environment this best represents the motivation, physiological imperatives and behavioural options for tunas foraging at fronts and that the resulting behaviour is as realistic as it can be.

4.4.2. Vertical Movements

Further simulations were then run in order to investigate vertical movements. Initially, food was made available in surface and deeper habitats. In this case, however, it was never profitable to forage at depth, presumably because encounter rates were much lower due to limited visual range. I then made food only available in the deeper, cold habitats. Varying the optimal temperature and metabolic rates provoked different patterns of behaviour, analogous to the differences between the behaviour of tropical and temperate tunas. The same representation of thermal stress that was used above was implemented i.e. thermal stress was incurred slowly, had a direct effect on fitness and recovery rate in warmer waters was rapid (see Eq. 4.7b, Fig. 4.3). The behaviour that results is analogous to that of tropical tunas, with most time spent in the surface waters and occasional excursions into deeper, colder waters (Fig. 4.10). In the second case, metabolic rate and optimal temperature for Albacore were used, both of which are significantly lower than those of Skipjack (Table 3.4). ARTU then spent most time in deep waters with occasional vertical excursions to surface waters (Fig. 4.11). This is consistent with the behaviour of adult Albacore, as well as the depth-tolerant behaviour of Bigeye and Bluefin, for which metabolic rate measurements are not available.

Fig. 4.5 Foraging simulation with no direct effect of thermal stress (i.e. $q_4 = 1$). The top graph tracks the bioenergetic state dynamics, the next 2 graphs track optimal habitat and swimming speed respectively, and the bottom graph tracks thermal stress Q. Habitat characteristics vary across the front (Table 4.1). The fish is predicted to inhabit the cooler, food-rich waters of Habitat 2 most of the time, increasing its swimming speed to actively forage during daylight hours. Because there is no direct effect of Q the fish can stay in Habitat 2 even under high stress levels. This is not very realistic and so a direct effect of Q on fitness was implemented
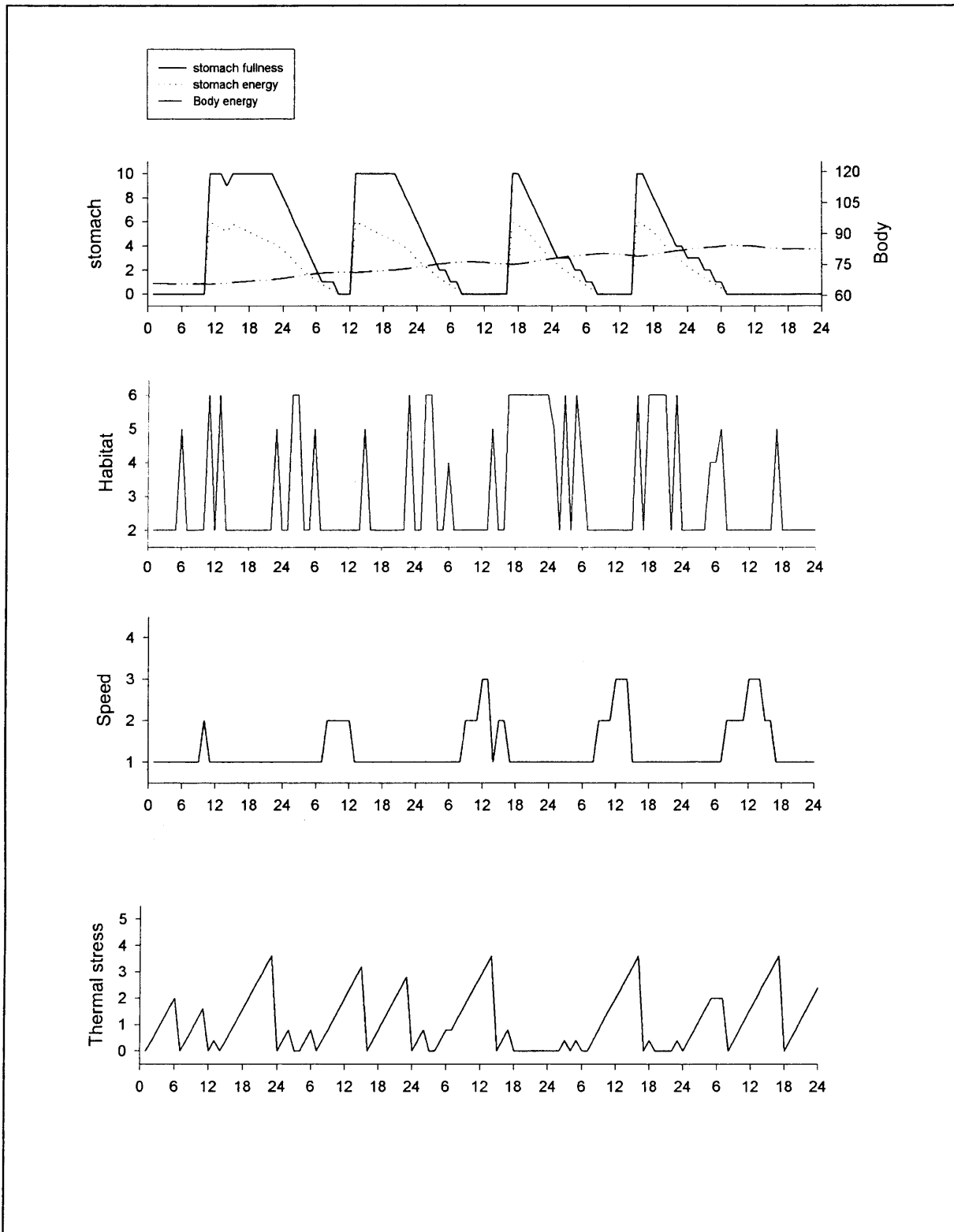
Fig. 4.6 (a) Optimal habitat and (b) optimal swimming speed for varying time and hunger state (stomach fullness); body energy is low (72 MJ) and thermal stress is zero. The implementation of a direct linear effect of Q on fitness leads to very conservative behaviour, with active foraging only predicted from 10:00–14:00 hrs when the stomach is completely empty. At all other times the fish should stay in Habitat 4
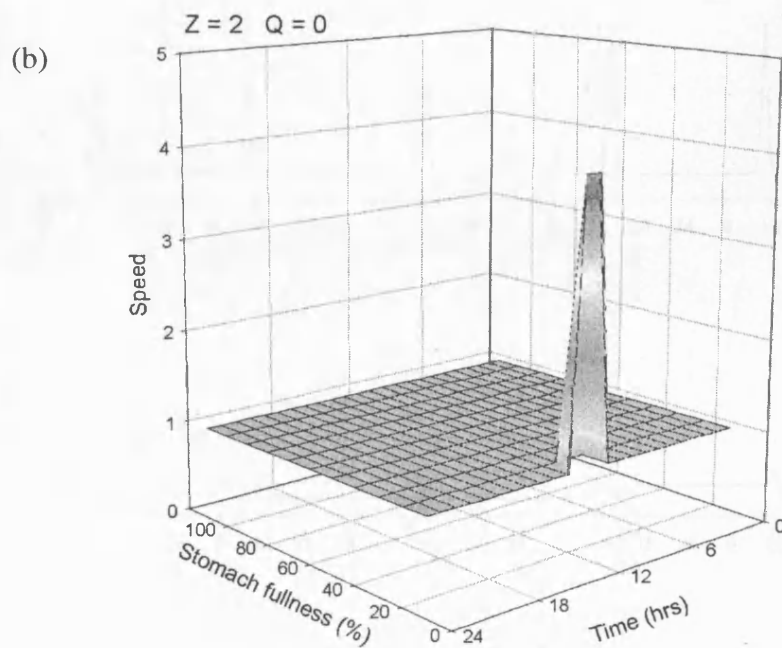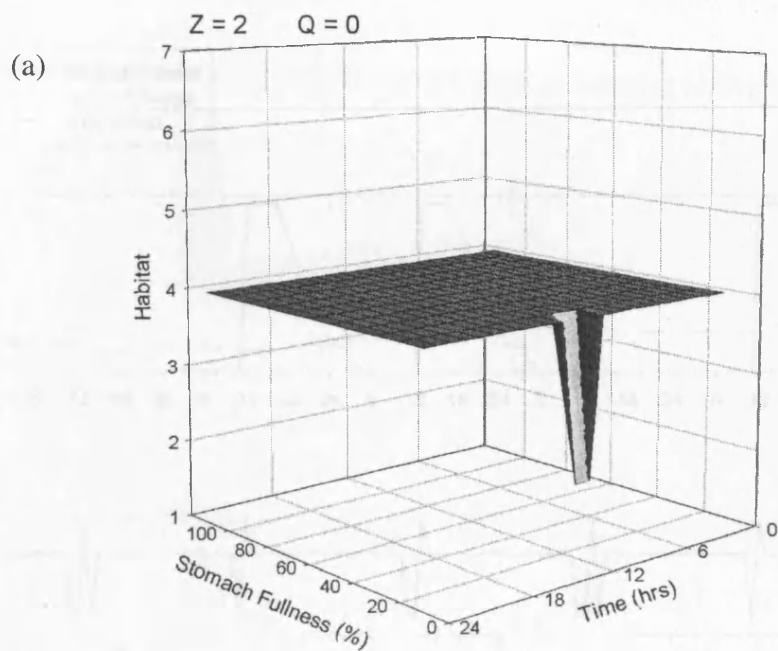
Fig. 4.7 Foraging simulation for the direct linear effect of Q on fitness. Time spent in colder water is extremely limited (1–2 h). This behaviour seemed overly constricted and so a direct quadratic effect of Q on fitness was subsequently implemented
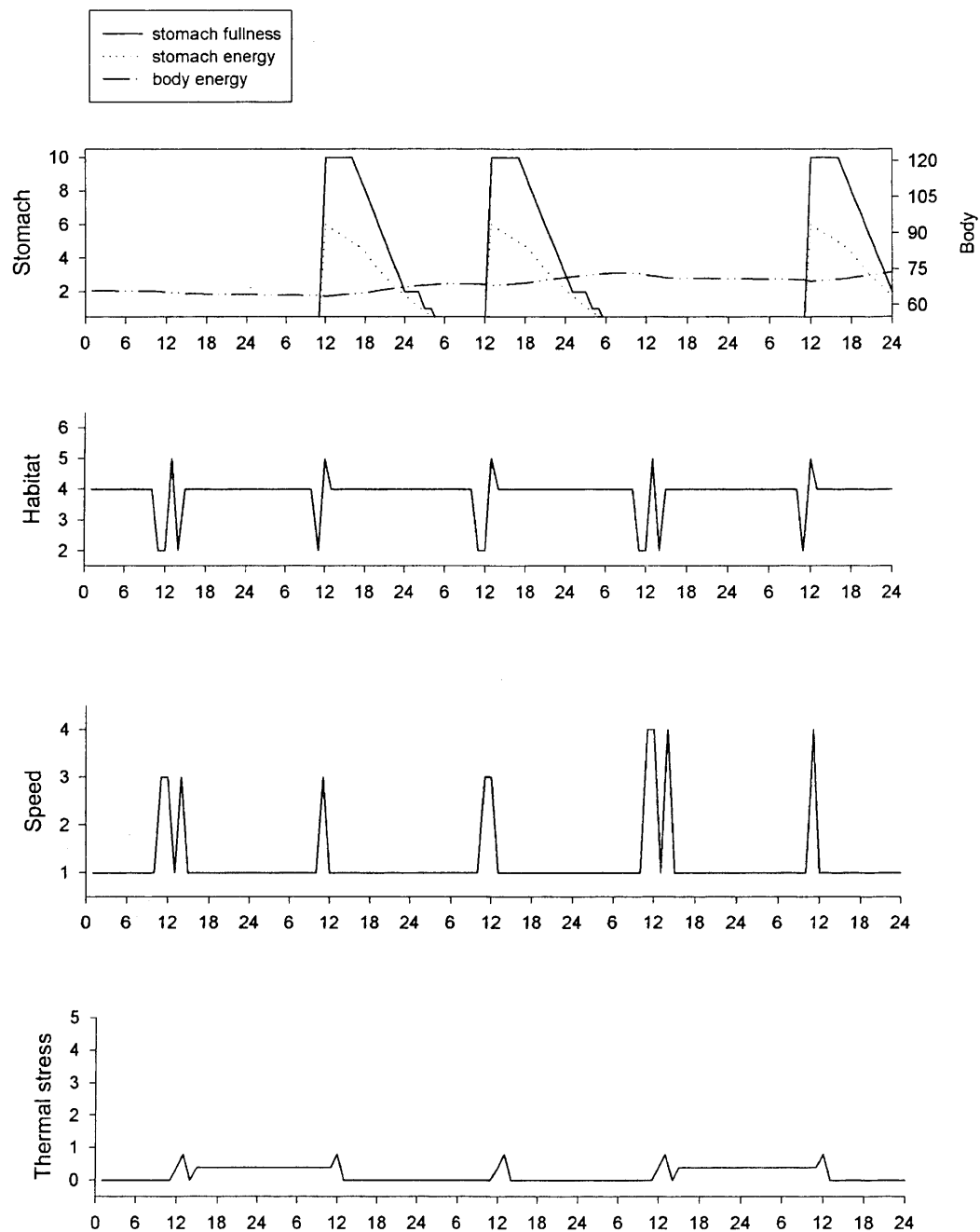
Fig. 4.8 (a) Optimal habitat and (b) optimal swimming speed for varying time and hunger state (stomach fullness); body energy is low (72 MJ) and thermal stress is zero. The implementation of a direct quadratic effect of Q on fitness leads to less conservative behaviour, with active foraging predicted from 07:00–17:00 hrs if stomach fullness is less than 70%. At most other times the fish should stay in Habitat 4, unless it still has food in its stomach prior to dawn; then it should seek warmer waters where digestion is more efficient and it may absorb stomach energy more quickly before foraging again
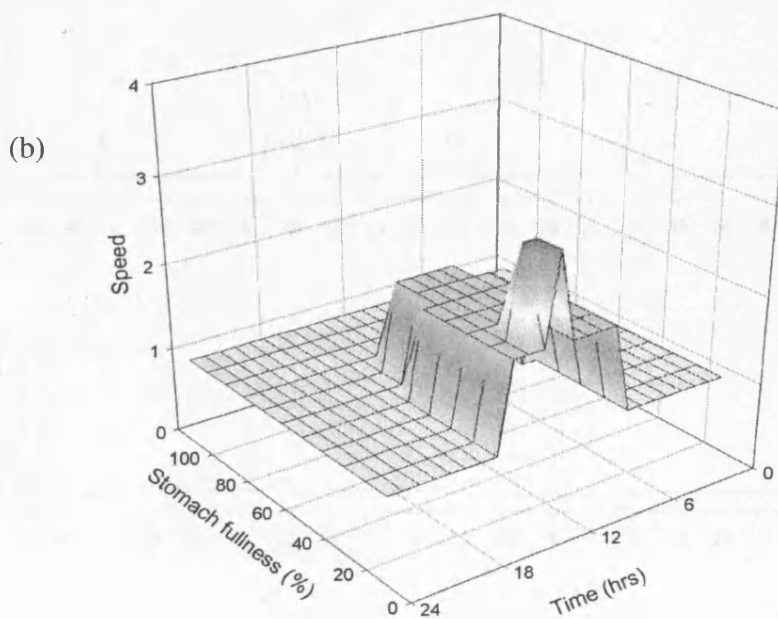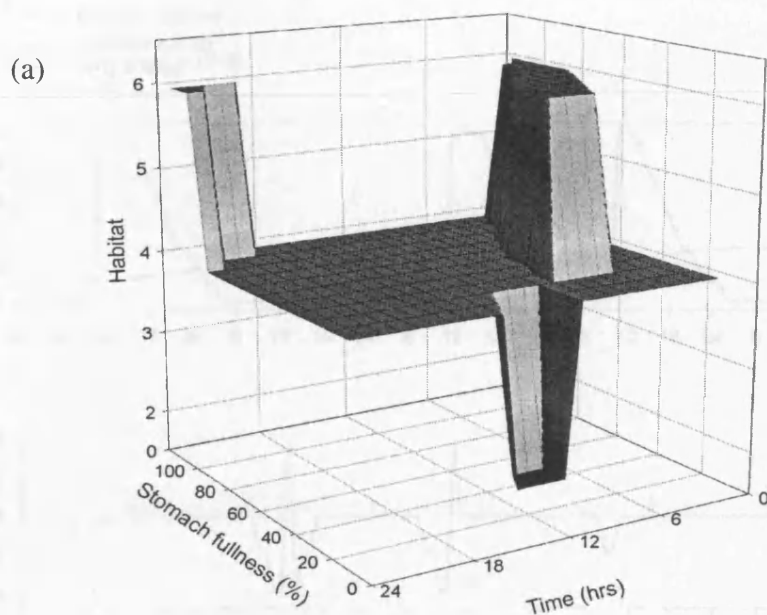
Fig. 4.9 Foraging simulation for the direct quadratic effect of Q on fitness. Time spent in colder water is less limited (1–6 h). This behaviour is more realistic
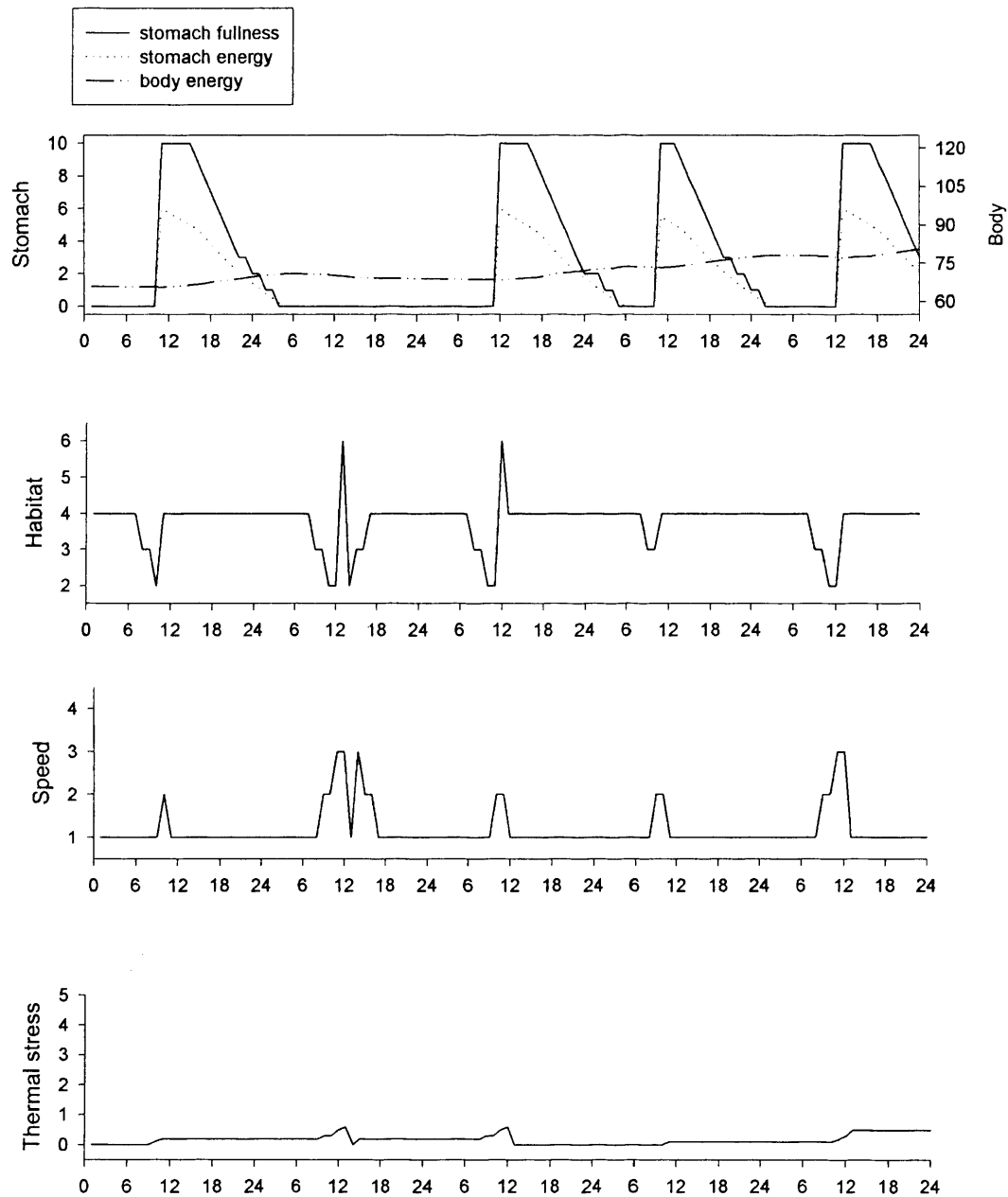
Fig. 4.10 Foraging simulation for vertical movements. Only the open ocean habitats are available. Food is only available in deeper waters, where the temperature is 8° less than the surface. With metabolic rate and optimal temperature similar to Skipjack and Yellowfin, ARTU spends most of the time in the surface waters, with short excursions to deeper water to forage.
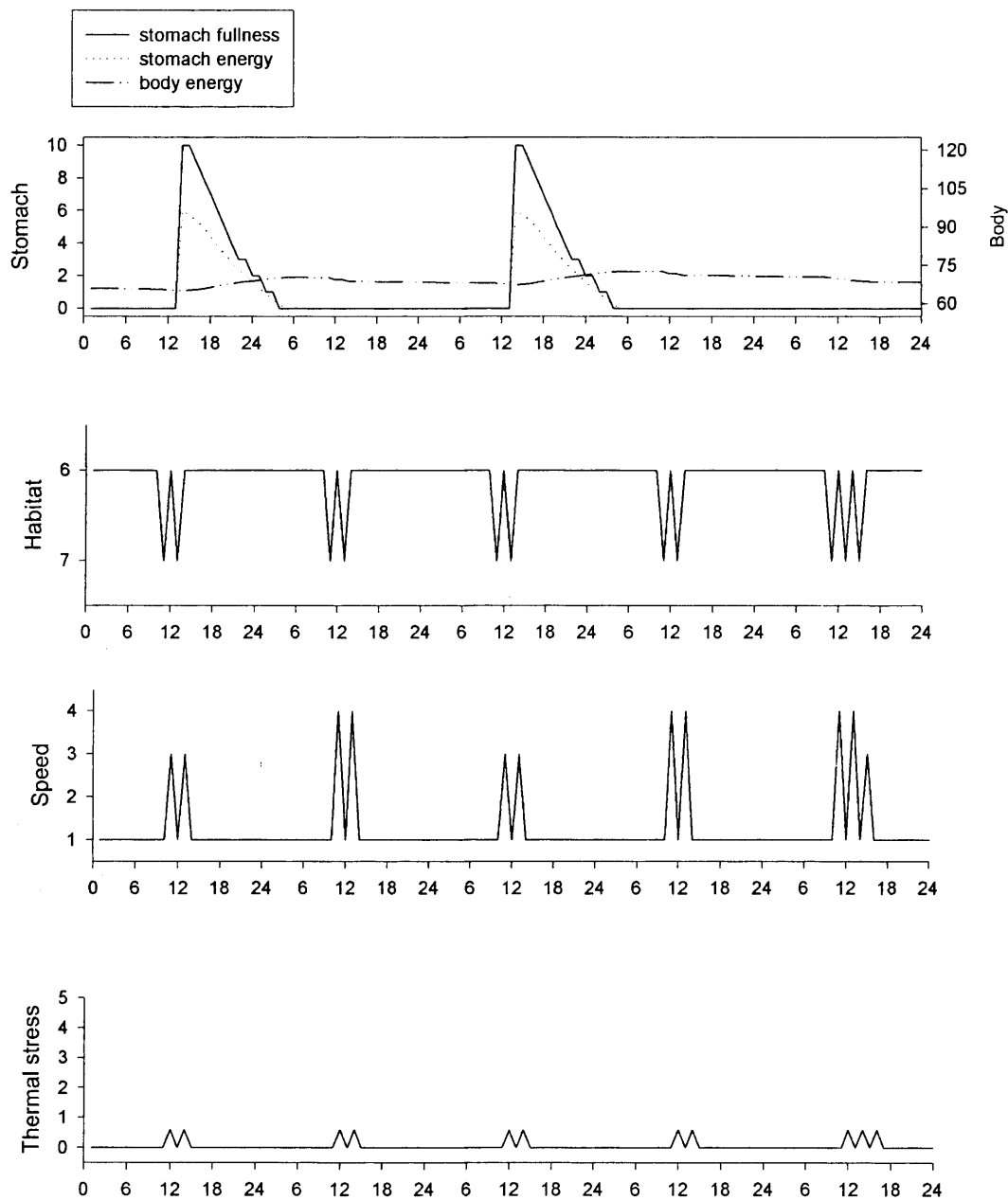
Fig. 4.11 Foraging simulation for vertical movements. Only the open ocean habitats are available. Food is only available in deeper waters, where the temperature is 8°C less than the surface. With metabolic rate and optimal temperature similar to Albacore, ARTU spends most of the time in the deeper waters with short excursions to shallow water to obtain a 'gulp of heat' (cf Brill 1994a)
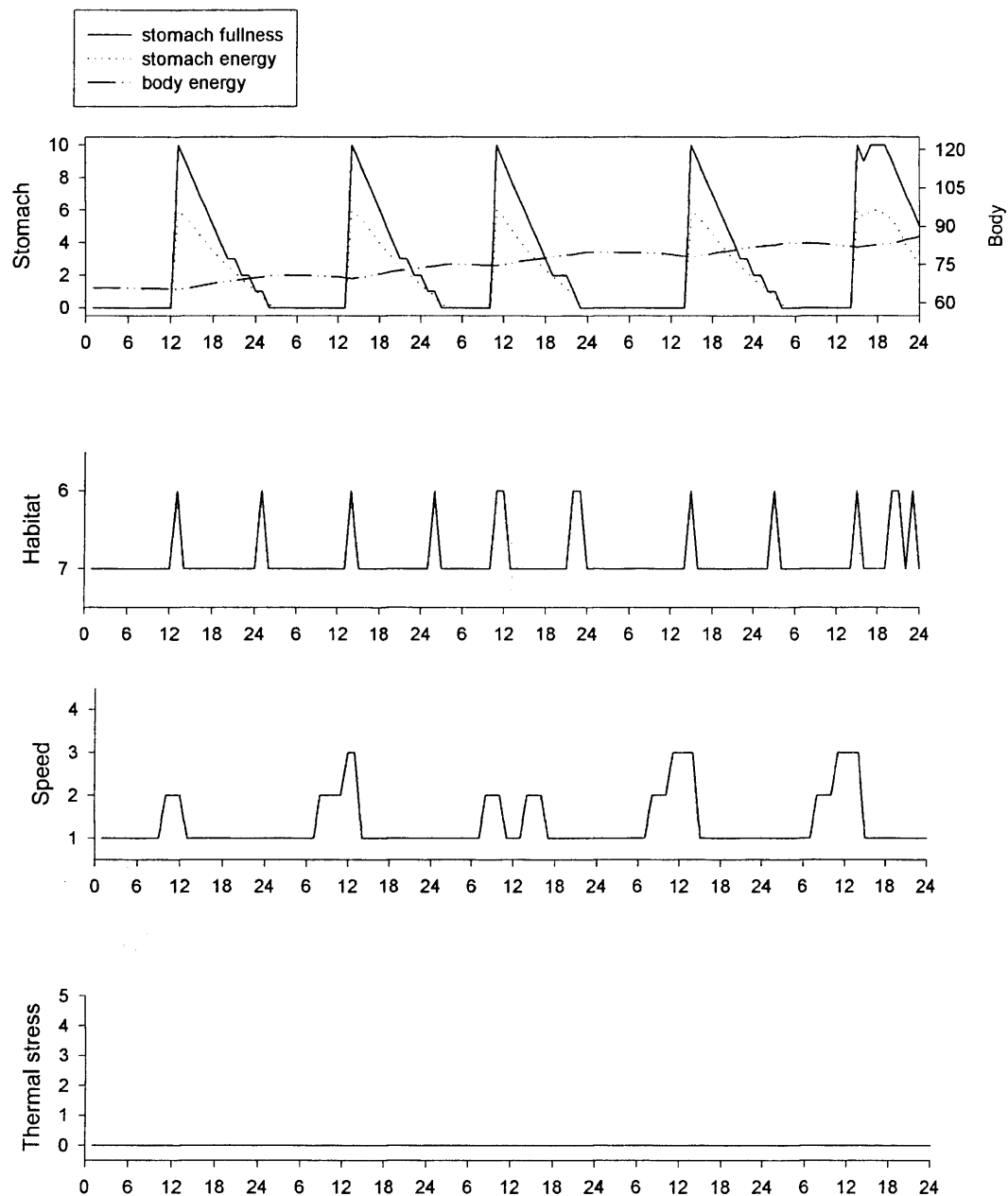
4.5. DISCUSSION

The main achievement of this model is the integration of environment, physiology and behaviour within a single, quantitative framework, thus providing a theoretically sound perspective from which to make and try to understand observations. I was able to make realistic simulations of observed behaviour by having a slow increment and fast decrement of thermal stress, representing the well-documented thermal inertia of tunas (Neill et al. 1976, Holland et al. 1992), and by including the effect of thermal stress directly on fitness. In reference to the questions asked at the start of the exercise (p. 78) I can say that the observed aggregation of tunas at ocean fronts is not predicted by temperature alone, and when turbidity is high on the cold side of the front it is not profitable to be in those waters unless they are higher in food abundance or quality than the warmer waters. By varying optimal temperatures and the representation of thermal stress in the determination of fitness, it was possible to generate differences in behaviour that are akin to the observed differences between surface dwelling tropical tunas such as Skipjack and Yellowfin and deeper foragers such as Bigeye and Bluefin. The model has therefore met its design criteria by representing mechanism and process to the best of our knowledge, and predicting behaviour from physiology. Its structure and detail are biologically meaningful, and its predictions are, in principle, measurable.

An inherent property of dynamic optimisation models is that at each stage, the individual has perfect knowledge of the fitness values of its present and future states and the consequences of alternative behaviours. Learning and physiological cues would explain knowledge of the past and present, and olfactory sense could be offered as an explanation for knowledge of future prey concentrations, through medium to long-range detection of prey prior to visual encounter (Atema 1980, Atema et al. 1980). The encounter rate between predator and prey is then determined by the visual feeding model (Aksnes & Giske 1993, Aksnes & Utne 1997). This is yet to be fully parameterised for tunas. It would be necessary to measure the visual capacity and sensitivity threshold of tuna eyes, as well as to characterise the inherent and apparent contrasts of their prey.

The model also makes predictions regarding state-dependent behaviour that have not yet been investigated in the field or laboratory. Simultaneous measurements of both state and environmental variables (stomach contents, heart rate, temperature, light) as well as the behaviours predicted (location, swimming speed, swimming mode) would provide a more detailed picture of the behavioural ecology of tunas than presently exists. Some work has been done in this area (e.g. Holland et al. 1992, Brill et al. 1999) but in no study have all relevant variables been measured simultaneously. By contrast, for Weddell seals *Leptonychotes weddelli*, heart rate, body temperature, depth and swimming velocity have been measured during free-diving, while a peristaltic pump withdrew blood samples and injected radio-labelled metabolites (Guppy et al. 1986, Hill 1986). Although more difficult for fish than mammals, such work could be repeated for tunas with measurements logged and transmitted by acoustic or satellite telemetry (e.g. Lutcavage et al. 1999).

The degree of convergence between model predictions and observations to date is encouraging but there are sufficient gaps in our present understanding of tuna biology that its predictions must only be seen as what could be achieved with further development and accurate parameterisation. Better information on the interplay of vital rates would justify more detailed modelling efforts. A smaller time-step than that used (1 h) would allow burst and cruise swimming to be more clearly resolved and additional habitats would add spatial resolution. Food types and concentrations will vary over time and water mass structure is dynamic. There will be a time and energy cost associated with moving between discrete habitats, which would depend on the scale of the ocean front. Instant escape to a favourable habitat may not be possible, and this will limit foraging range. The conservative nature of the behaviour predicted here may therefore be an artefact of the model environment. The main limit to implementation of a more dynamic physical scenario is the 'curse of dimensionality' whereby the task of solving all possible solutions becomes computationally overwhelming. The effect of this can be limited by interpolation of the state dynamics (Mangel & Clark 1988) but a fully 3-dimensional physical oceanographic model would increase the overall

dimensionality of the model beyond the scope of the computational power available to the us. An individual based dynamic optimisation model with stochastic prey encounter, such as has been derived here, has its limits and it would be necessary to use alternative techniques to investigate the complexities of group dynamics and its fitness consequences. Progress would indeed be made if we could simulate density-, frequency- and state-dependent aspects of behaviour in a single foraging model with the level of mechanistic detail incorporated here but in a more physically realistic model environment. For this to be achieved, an adaptation approach (Giske et al. 1998) for fish foraging in a time-varying oceanographic environment may be more suitable in terms of both tractability of derivation and computational efficiency.

Behaviour was simulated from individual motivation to optimise energy balance in the presence of various factors that must be traded off against each other. In life-history models, spatial population dynamics derive from evolutionary motivation through the use of a truly Darwinian fitness measure (e.g. Fiksen et al. 1995, Huse & Giske 1998). Further work, considering populations of individuals over large space and time scales should seek to interface the biophysical dynamics of the oceanic environment with fish behaviour motivated by evolutionary as well as physiological imperatives (see Chapter 5 for an attempt at this and Chapter 6 for extended discussion and proposals for further work).

4.6. CONCLUSIONS

An established paradigm in behavioural ecology, with an associated computational method, was applied to a new situation in order to investigate some fundamental questions about the foraging behaviour of tunas in relation to their environment. In doing this, competing hypotheses were brought together into a single model, thus improving our understanding of why tunas and other fish may aggregate at fronts. This work has been anticipated in the literature for some time (see p 30 of Hunter et al. 1986a) but has not previously been realised. By working from mechanism up, rather than from data down, it has been possible to predict time- and state-dependent optimal foraging behaviour (i.e. slow swimming in warm clear waters when not foraging, and foraging excursions into colder waters when hungry) that is broadly consistent with observation (Block et al. 1997) and other modelling work (Dagorn et al. 1995). Sharp & Francis (1976) commented that, 'The utility of simulation studies lies in the process of linking together observations, using generalised principles where possible, to generate testable hypotheses which ultimately lead to resolution of cause and effect relationships.' Here a modelling framework is suggested that, if developed further and properly parameterised, would allow testable hypotheses to be made and cause and effect relationships to be clearly resolved. Areas of research into tuna vision and physiology, which will facilitate progress in tuna behavioural ecology, have been identified, and investigations that will allow theoretical predictions to be tested for free-living animals have been suggested. I would emphasise the importance of time- and state-dependent aspects of behaviour, predicted by the model and observed in living tunas, and the need to identify and account for all relevant biological and physical properties of the ocean environment.

CHAPTER 5

A SPATIALLY EXPLICIT LIFE HISTORY

MODEL FOR PACIFIC SKIPJACK TUNA

CONTENTS

5.1. SUMMARY

In this chapter the biological properties detailed in Chapter 3, and ecological interactions incorporated in Chapter 4 are extended into a 'whole ocean' and 'whole population' scale. A life history model, which is driven by adaptation and evolution, has been developed in relation to environmental variables derived from satellite and *in situ* observation and from numerical simulation. The spatial domain is the Pacific Ocean. The time period studied is open-ended, with results depicted for 1 yr. The number of agents for which detailed biological modelling is carried out is ~2000; each agent represents up to 1 million individual fish, and mortality rates derived from environmental variables are applied.

The model is presented here as a proof-of-concept exercise. The methodology adopted for modelling fish behaviour is different from that used in Chapter 4. Programming techniques from the field of 'artificial life' are used to study 'real' life. There are few examples of these techniques applied to marine ecology yet they permit an important methodological synthesis, uniting oceanography and ecology within a framework that might find useful practical application in fisheries science. The aim is to show that it is possible to model fish population dynamics on a whole-ocean scale by deliberate inclusion of relevant biological detail such that interactions of individuals with the environment are explicitly considered in a mechanistic manner, as are the proximate and ultimate motivations for behaviour and spatial dynamics. The intention is to support a new approach in fisheries ecology that seeks management tools which are better-based on ecological theory and which incorporate interactions between individuals and their heterogeneous environment. Such work is likely to have a significant impact on fisheries forecasting methods; given the ever-improving capabilities of computing facilities and the ocean circulation and production models that can run on them, it will no longer be acceptable to ignore important ecological and evolutionary processes that impact on fish stocks.

5.2. INTRODUCTION

Studies of marine fisheries ecology are studies of complex adaptive systems. A system is considered to be complex when it is not possible to understand it through simple cause-and-effect relationships or other standard methods of systems analysis. Complexity theory is evolving from several major fields (mathematics, physics, biology, economics, organisational theory, computer science) in response to 2 realisations: that modern science often reflects only that part of reality which is observable, controllable, ordered, linear, and predictable; and that disciplinary specialisation runs counter to the major need for integration of knowledge in order to resolve contemporary issues, particularly those concerning resource management.

Spatially explicit modelling of fish population dynamics has been carried out in various ways (e.g. Bertignac et al. 1998, Huse & Giske 1998, Sibert et al. 1999). As yet the input of remotely sensed environmental data to the models remains limited. The advection-diffusion model of Bertignac et al. (1998), for the spatial population dynamics of Pacific skipack tuna, relies on earlier models for general circulation (Blanke & Delecluse 1993), biogeochemistry and new production (Stoens et al. 1998) and tuna forage production (Lehodey et al. 1998). Satellite data are input at different levels; weekly winds from the ERS-1 scatterometer are used to drive the circulation model; monthly chlorophyll climatologies from the CZCS are assimilated into the new production model. In this way the model as a whole is prognostic for tuna. Here I have used the same levels of oceanographic modelling for the Pacific Ocean as were used above (i.e. data derived from Blanke & Delecluse 1993, Stoens et al. 1998, Lehodey et al. 1998) but instead of a model based on an advection-diffusion equation (Bertignac et al. 1998, Sibert et al. 1999) I have developed a spatially explicit life history model using programming techniques from the field of 'artificial life'.

'Artificial life' (A-life) has emerged from the broader field of 'artificial intelligence'. The essential properties of living organisms (self replication and open-ended evolution, Ray 1995) are recreated in a model environment with at least some of the complexity of the natural environment. 'Autonomous agents' are used to simulate the behaviour of real animals;

these agents are further described as 'adaptive' when their competence can improve with experience (Maes 1995). Individual-based modelling in ecology and autonomous agent research have evolved independently yet there is increasing convergence between these fields (Taylor & Jefferson 1995, Parrot & Kok 2000, Huse et al. in press). In this work, a genetic algorithm (GA, Holland 1975, Goldberg 1989, Mitchell & Forrest 1995) is used to train an artificial neural network (ANN, Dayhoff 1990, Hertz et al. 1991, Anderson 1995) within an individual based model (IBM, DeAngelis & Gross 1992, Tyler & Rose 1994, Grimm 1999, Huse et al. in press). This approach has recently been developed and described by Huse (1998), Huse & Giske (1998), Giske et al. (1998) and Huse et al. (1999). Both ANNs and GAs were inspired by biological phenomena (i.e. stimulus–response, learning, adaptation, evolution) yet they have a much longer history in technological and industrial applications than they do in the study of natural systems. The GA is an optimisation technique based on evolution by natural selection; it is a heuristic method, seeking optimal solutions by trial and error, through selection of good solutions and removal of weakly performing ones. This compares with more mathematically exact methods of optimisation (e.g. SDP, Chapter 4), where risks and expected gains are calculated for all possible decisions, with reference to a pre-determined goal. ANNs are intentional, simplified mimics of organic nervous systems (Anderson 1995, Ray 1995). Behavioural output is obtained from differential weighting of input variables (Rummelhart et al. 1986, Montana & Davis 1989, Huse et al. 1999). ANNs may be constructed with a variety of different architectures (Dayhoff 1990, Hertz et al. 1991). Engineering and other problem-solving applications of ANNs might use whatever complexity is deemed necessary, and the structure of an ANN may itself be allowed to evolve (Rechenberg 1994). Here the structure is kept simple and biologically meaningful, which is perhaps most important given the context of the work (see SUBROUTINE MOVEMENT).

It is not unusual in IBMs to only allow adults with a certain 'fitness' (e.g. fecundity) to reproduce. Here the concept of 'endogenous fitness' is applied (Strand et al. unpubl.) whereby any adult may reproduce and its fitness is never explicitly counted; its offspring will only be

able to reproduce if the new SV (chromosome) carries weights (genes) that result in a successful strategy that allows survival and growth through to the adult stage. This approach is less prescriptive than others and closer in process to evolution by natural selection. This approach avoids arguments concerning the potential tautology of the phrase 'survival of the fittest', depending on how fitness is defined, by not defining fitness at all. Flexibility in life history strategy is essential for ongoing proliferation of any individual gene. What may constitute fitness in one environment may not be so fit as the environment or as biotic factors such as predation, parasitism or competition also change. Adaptive models are therefore well suited to studying the effects of environmental change and stochasticity.

5.2.1. Input data

Monthly climatological data for relevant environmental variables were used as input data for the skipjack life history model. These data were provided by P. Lehodey (Secretariat of the Pacific Community, New Caledonia) and consist of zonal and meridional currents from an ocean general circualtion model (u and v respectively, Blanke & Delecluse 1993), sea-surface temperature (SST, Levitus & Boyer 1994), surface chlorophyll derived from the CZCS (cphyll, Tran et al. 1992) and an index of tuna forage (i.e. prey) concentration (Lehodey et al. 1998, Bertignac et al. 1998). The data resolution is $1° \times 1°$ and the model domain is 49.5°N to 39.5°S and 110.5°E to 70.5°W.

Input data were first 'unzipped' and then checked for any obvious errors and missing values. A FORTRAN program (INPUT) was written for this task (Appendix II). This program reads in the data in the format provided, converts CZCS color value to chlorophyll concentration (mg m^{-3}), bounds the domain by flagging land and cells permanently contaminated by cloud, and then fills in missing data by spatial interpolation (arithmetic mean of neighbouring cell values) or temporal interpolation (value for preceding month). Data are available for all grid cells in the ocean except in the case of CZCS chlorophyll, where missing values result from proximity to land and from cloud coverage. In this model, fish must still be able to move into cells that exist in physical space but for which no data exist. Interpolation

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was therefore necessary. However, it was only carried out for cells where values for SST existed (i.e. definitely in the ocean). The percentage of cells requiring spatial and temporal interpolation were 1.5% and <0.01% respectively.

5.3. THE MODEL

The model was written in FORTRAN programming code (Appendix II) using Microsoft Developer Studio, provided by A. Kirby, Microsoft Corp. Modelling the individual characteristics of a population of several billion individuals would take an infinite amount of time to process. Instead a population of ~2000 'super-individuals' is used, which live as if they were sole individuals; mortality functions then operate on the number of sole individuals represented, rather than just on the super-individual itself. When the number of individuals represented falls to zero, the super-individual ceases to exist. A super-individual therefore represents the compromise necessary between biological realism and computational convenience. In this work, super-individuals are referred to as 'fish', with the understanding that they are actually adaptive autonomous agents in a model representation of a real complex system. Each fish has characteristics stored in 2 vectors. The 'attribute vector' (AV) contains biological properties (i.e. age, length, weight, energy density), the number of individuals in the super-individual and the position of the fish on the grid. The 'strategy vector' (SV) carries the weights of the ANN, which determine the behavioural responses to environmental stimuli (for further details see Huse et al. in press). When a fish dies, its SV is removed from the 'gene pool', and the super-individual is assigned to a batch of freshly-spawned larvae, with an SV derived from its parents (see SUBROUTINE REPRODUCTION).

PROGRAM SKIPJACK

This is the main program that initialises the loop variables (population, year, month, day etc.) opens and closes log and output files, and calls the subroutines that contain the detailed physiological and behavioural calculations. The random number generator is seeded, initially using a fixed, odd numbered integer value for comparability among simulations.

The first 2 subroutines (INITIALISE and ENVIRONMENT) are called once, at the start of the program. The others (GROWTH, MOVEMENT and REPRODUCTION) are called each timestep (i.e. day).

SUBROUTINE INITIALISE

This subroutine initialises the strategy and attribute vectors of each fish in the population and specifies the number of days in each month of the year. The SV is initialised by random weights between 1 and −1. The AV is initialised as follows. All fish are declared alive and assigned an age between 90 and 810 d. Each fish represents 1 million individuals. Body length is derived from age using a Von Bertalanffy calculation (Sibert et al. 1983, Hampton 2000), body mass is derived from length using an allometric relationship (Murray et al. 1999) and body energy is calculated as the product of body mass and energy density for healthy skipjack (6 kJ g^{-1}, Boggs & Kitchell 1991). All fish are assigned intitial locations in the central, equatorial Pacific.

SUBROUTINE ENVIRONMENT

Input data (sst, forage, cphyll, u, v) that have been 'groomed' using an earlier program (described above) are now input to the model. They are read in as temporary variables and then assigned to labelled arrays, with actual latitude and an index for longitude (1–180), thus avoiding any problems regarding the coordinates of the date line. All grid cells that have incomplete time series for SST or cphyll at this stage are flagged as land. Any fish that has inadvertently been initialised on land is moved into the sea and maximum values for all environmental variables are recorded for use in standardising data input to the ANN.

The model runs on a daily time step but the environment data are monthly climatologies. To circumvent potential problems associated with artificial stability during the month and a large jump at the transition between monthly mean values, the monthly mean data are converted to daily values by linear interpolation between months. Despite the convenience of assuming a year length of 360 d (i.e. 12 mo each of 30 d) as is convention in oceanography, the actual number of days in each month is used. This may be important in the

use of climatologies for months of varying lengths. In order not to use up too much memory, daily data are not themselves stored, but the daily increment/decrement is calculated and this value is stored along with the monthly mean; daily data are then calculated as needed.

SUBROUTINE GROWTH

This is the main routine containing biological detail, which modifies the attributes of the fish through ecological interactions and physiological processes. Daily values for environment data are calculated by assigning the climatological value to the 15th day of the month, and then calculating: monthly mean ± (daily increment ×days), where days is the number of days since the 15th day of month 1.

The nature of ANN methodology is that the networks need to be 'trained' to solve the problems that they are confronted with. In this case the weights of the ANN are evolved using the GA, but in order to ensure that sufficient fish remain viable in the model for long enough to allow proper training, all mortality functions are modified by a coefficient for 'training decomposition' (TD) that reduces mortality during the early years of the simulation.

The fish are classified into 2 age groups: planktonic larvae and nektonic juveniles/adults. Planktonic larvae are those fish less than 90 d old. These have no swimming ability and just drift with the currents (see SUBROUTINE MOVEMENT). Their length is determined from their age by the Von Bertalanffy equation (Sibert et al. 1983, Hampton 2000). Coefficients are derived for 3 mechanisms of natural mortality, each of which relates to environmental variables in a different way: predation (MPred = forage index / length), starvation (Mstarv = 0.025 / cphyll) and temperature stress (MTherm = 0.025 × δT,where δT is the difference between actual and optimal SST). The relative contributions of these different mechanisms of natural mortality for fish larvae have never been quantified in the field but the absolute magnitude of their combined effect is within the range of observed values (Peterson & Wroblewski 1984, McGurk 1986, Davis et al. 1991). These mortality coefficients are summed and applied to the number of individuals represented by the fish.

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The same components of natural mortality act on nektonic juveniles/adults as on planktonic larvae but the ways in which the coefficients are estimated differ. Length based mortality applies until the fish has reached 30 cm, after which predation is considered to be negligible. Mortality due to thermal stress still applies, but the limits set for this are fairly broad (optimal temperature range for larvae and adults is 20–30°C). The nekton stage is considered to be non-bouyant, and detailed bioenergetics (SMR, AMR, growth and reproduction) and prey encounter calculations are carried out. SMR and AMR are calculated as described in Chapter 3 (p 3.17/8). The daily time step is divided into 2 periods (day/night). Skipjack are assumed to be foraging during daytime and not foraging at night; they are therefore assigned swimming speeds of 3 and 1 body lengths s^{-1} during these respective periods. There are 2 feeding bouts (i.e. stochastic prey encounters) permitted in each daytime period. Visual range depends on water clarity (Eq. 3.4), which depends on chlorophyll concentration ($k_{490} = 0.022 + 0.119 \times$ cphyll$^{1.122}$, Austin & Petzold 1981). Whether or not a meal is obtained during each feeding bout is determined by drawing a random number from the system and comparing this number with the probability of finding food during this time, determined by Eqs 3.5/6. If a meal is obtained, the energy content of the fish is increased by the product of mass ingested (5% of skipjack body weight, Table 3.4) and the energy density of the prey (7 kJ g^{-1}, Boggs 1991), and decreased by SMR, AMR and SDA; if a meal is not obtained, energy cost does not include SDA.

Growth of the skipjack is modelled using the concept of 'structural weight' (Rosland & Giske 1997). Increased body mass follows a surplus energy budget by assuming constant energy density for 'healthy' skipjack (TED, 6 kJ g^{-1}, Boggs & Kitchell 1991; body mass = body energy / TED). Subsequent energy losses result in a decrease in energy density rather than body mass, as water content increases during starvation (Boggs & Kitchell 1991). If the fish then feeds, it must recover its energy density to the 'healthy' level (i.e. TED) prior to further growth. Fish length is calculated from structural weight by an allometric relationship (Murray et al. 1999).

Once the energy budget has been calculated, mortality functions are applied. Starvation is now a function of energy density, reflecting feeding/activity history rather than immediate food availability. The mortality coefficient (Mstarv) is derived such that it is 1 for critically low energy density (3 kJ g^{-1}) and 0.1 for healthy skipjack. Spatially-uniform length-based fishing mortality is applied, as is mortality due to senescence, for those skipjack > 3 yr old, using mortality coefficients calculated from tag data (Hampton 2000). Finally, the fish is removed from the population if, after all mortality coefficients have been applied, there are no longer any individuals represented.

SUBROUTINE MOVEMENT

In this routine, the positions of the skipjack in the Pacific ocean are recalculated and updated based on the surface currents experienced and, in the case of juveniles/adults, on directed movement decisions as output from the ANN. Daily values for environmental variables are derived from climatologies, as in SUBROUTINE GROWTH. For the surface current components (u, v), values are determined for the 4 corners of each cell and the actual current experienced by the fish, located at a defined position within the cell, is determined through bilinear interpolation (Adlandsvik & Hansen 1998). The advective distance is calculated i.e. the displacement of a passive drifter by the velocity vector during this time step. The velocity vectors are in cm s^{-1} and must therefore be converted first to km and then to degrees, in order for the new position to be assigned. Because of the large scale of the model domain, it is not realistic to assume a flat Earth (i.e. 1° lat./lon. = 111 km) and so the conversion from distance (km) to degrees lat./lon. takes into account the latitude of the fish by 'Great Circle Path' calculation i.e. 1° lon. = 111 ×cosine (lat.) km. For larvae, the new position at the end of the time step is simply the old position modified by the current vector integrated over 24 h. For juveniles/adults, the new position is determined by the ANN.

The ANN is a feed-forward network with 1 input layer (6 nodes), 1 hidden layer (3 nodes) and 1 output layer (3 nodes) (Fig. 5.1). The number of nodes used depends on how much information we want to give the fish (input) and what decisions we want it to make

(output). The input variables could be anything that might be important to the fish. The fact that the programmer can control this is a significant advantage over traditional optimisation techniques (e.g SDP, Chapter 4), which by necessity imply full knowledge not only of the attributes of all available environments but also of the fitness consequences of all possible decisions. All of the variables chosen here as input data, including those that are external (position, temperature, forage) and those that are internal (time, condition), may be sensed by fish that are as well adapted to the pelagic environment as are skipjack.

Fig. 5.1 The ANN architecture used in the model. Input variables are those that a skipjack might realistically sense in the ocean; ouput variables are those simple choices available regarding movement and reproduction

INPUT LAYER　　　　**HIDDEN LAYER**　　　　**OUTPUT LAYER**
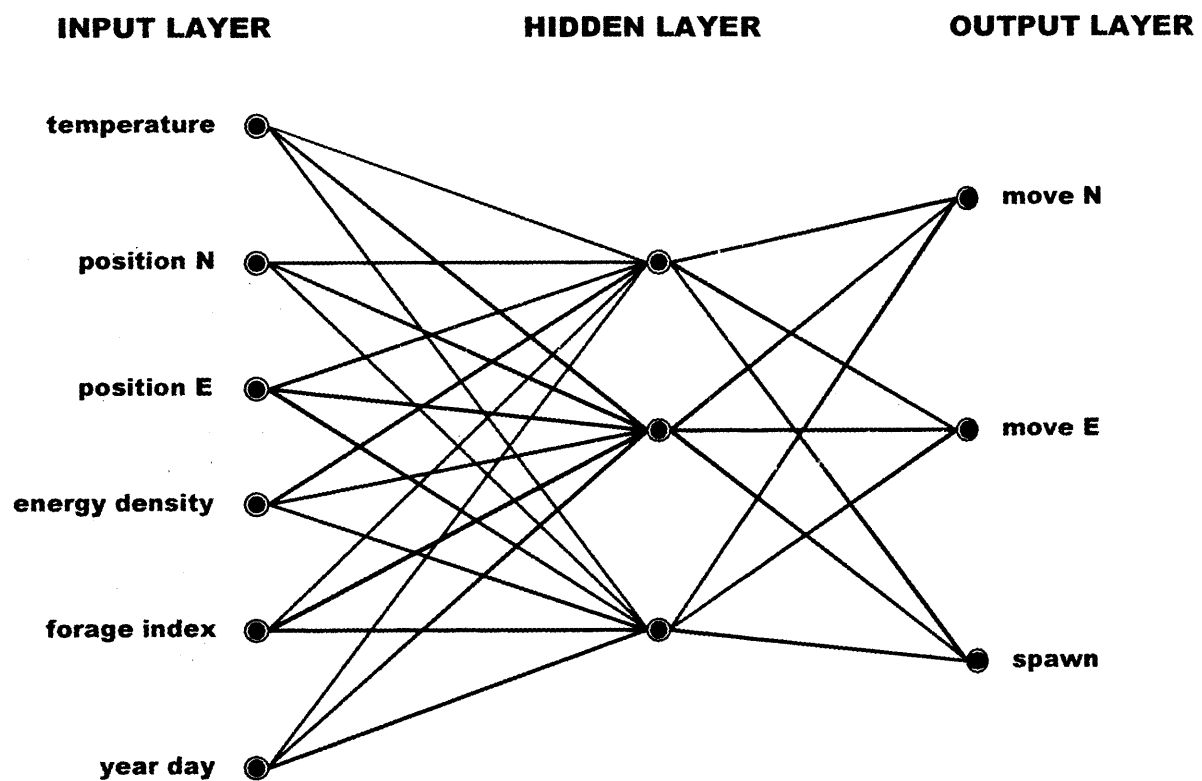
The hidden layer allows non-linear (and non-determined) interactions among variables. For each hidden node the sum of the products of the standardised input values and their respective weights in the strategy vector is calculated. This sum is then sigmoid-transformed and weighted by the connection strength between the hidden and output nodes. At the output node the values are again summed and transformed, thus providing the output decision. The output variables are simply the direction of movement and the decision to spawn. Each node for direction can take 1of 3 values (−1, 0, 1) resulting in 9 possible directions, including the

option to stay in the same location. The decision to spawn is simply a yes/no (i.e. 1 or 0). These logical outcomes are achieved by transformation of the weighted sums at each node by sigmoid activation functions, scaling the output either from 0 to 1 (2 options) or −1 to 1 (3 options). The distance moved depends on the body length of the fish and on the current field. Swimming behaviour is simplified in SUBROUTINE GROWTH to a 12 h cruising period (night, 1 body length s^{-1}) and a 12 h foraging period (day, 3 body lengths s^{-1}); average swimming speed over a 24 h period is therefore 2 body lengths s^{-1}. The directed movement vector is the combination of the direction of movement, output from the ANN, and the daily distance of: $(24 \times 60 \times 60) \times 2$ body lengths d^{-1}; this is combined with the advection vector to give the resultant total movement vector, and the new position is then calculated. Error checking is carried out to ensure that the skipjack do not move onto land.

If the model has reached the time horizon (i.e. the desired end of the simulation) output files are written from this routine. These are written on a daily basis and sum the number of fish in each cell. Environmental variables may also be output for visualisation at this stage.

SUBROUTINE REPRODUCTION

For the sake of simplicity the model fish have only 1 sex; because there is more published information available, bioenergetics and fecundity calculations are carried out as for female skipjack. In reality, males are expected to maintain the same high frequency of spawning but without such high energy costs. They are consequently able to grow slightly larger than females. Here, the onset of maturity is taken to be at body length 42 cm (Stequert & Ramcharrun 1996), relative batch fecundity, in terms of number of eggs per spawning body weight, is ~100 eggs g^{-1} (Matsumoto et al. 1984, Stequert & Ramcharran 1995) and the energetic cost of spawning is 2% of body weight/energy (Hunter et al. 1986b).

The model equivalent of 'genes' are the weights of the ANN, which are carried in the strategy vector (SV, cf chromosome) of each fish. These are fixed throughout the lifetime of the fish and determine how it should respond to the environmental conditions encountered, as well as the other input variables (time, position and condition). At the point of reproduction,

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the GA is used to form a new SV from recombination of 2 parent SVs and from an element of random mutation (Fig. 5.2). Thus the process is analagous to sexual reproduction, requiring 2 parents and affecting the genes of a single chromosome.

parent 1	0.74	−0.39	0.22	0.43	−0.80	0.12	...
parent 2	0. 41	0.95	0.76	−0.37	−0.56	0.02	...
			RECOMBINATION				
offspring	0.74	−0.39	0.22	−0.37	−0.56	0.22	...
						MUTATION	
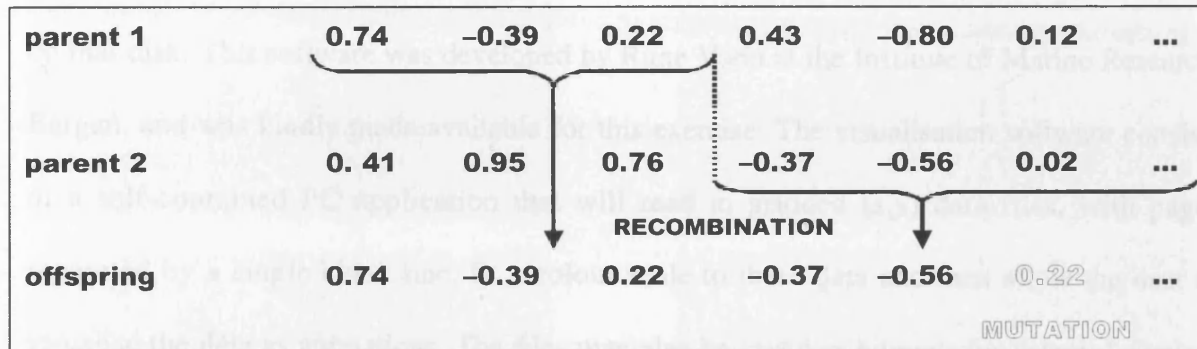
Fig. 5.2 Reproduction by crossover, mutation and recombination of parent strategy vectors. In this way, successful strategies (i.e. those that have resulted in the fish surviving to this stage) are passed on to the next generation, without reference to any predetermined fitness measure i.e. fitness is 'endogenous'

On entering this subroutine the fish are evaluated for whether they are sexually mature and whether the decision to spawn was activated by the ANN in SUBROUTINE GROWTH. If these conditions are met then a partner is drawn at random from those fish in the same grid cell that have also decided to spawn. Both parents are then penalised with a 2% loss of body energy. The SV of the offspring is formed by recombination of the 2 parent SVs, with crossover occurring after a random break point (Fig. 5.2). There is then a small probability that any of the new 'genes' may mutate into a different random number.

Once the SV of the offspring has been determined its attributes (AV) are assigned. The initial AV does not represent the true characteristics of the offspring, except for position and number of individuals represented, because the new 'fish' is actually a batch of planktonic larvae. However, the attributes that will apply once the fish becomes nektonic are nevertheless initialised here and then not used until the nekton stage.

5.4. RESULTS

At this stage, the main result of this work is the successful development of the model such that it actually runs through from input of environmental data to output of fish distributions. The FORTRAN code developed is presented in Appendix II, and input/output data are contained on the ZIP disk supplied; these can be visualised using software contained on that disk. This software was developed by Rune Vabo at the Institute of Marine Research, Bergen, and was kindly made available for this exercise. The visualisation software consists of a self-contained PC application that will read in gridded (x,y) data files, with pages separated by a single blank line, fit a colour scale to these data and then allow the user to visualise the data as animations. The files may also be saved as bitmaps for external display. A series of these output files is presented in Fig. 5.3.

5.4.1 Protocol for visualisation of environmental data and model output

Copy the file **animator.exe** to your hard disk and double-click to start the program

Go to **settings — set parameters**

Enter a grid size of: **180   90   1**

with **360** pages if viewing the model output or **12** pages if viewing environmental data

Then click **OK Open File**

Find the data file **SKJ.txt** for model output or **AN_*.txt** for environmental data and double-click to open it in the animator. A progress bar and dialogue will state how many pages have been read. When this is complete go to **options — enable scaling** and on the left side of the display move the **set scale** slider to the left, until the scale is set to **2.5**

Then click **animate** to see the results

For repeated and faster animation go to **images — generate bitmaps**

When the animation is complete click on the red button to loop through the bitmaps

To save any particular bitmap to file go to **images — save**
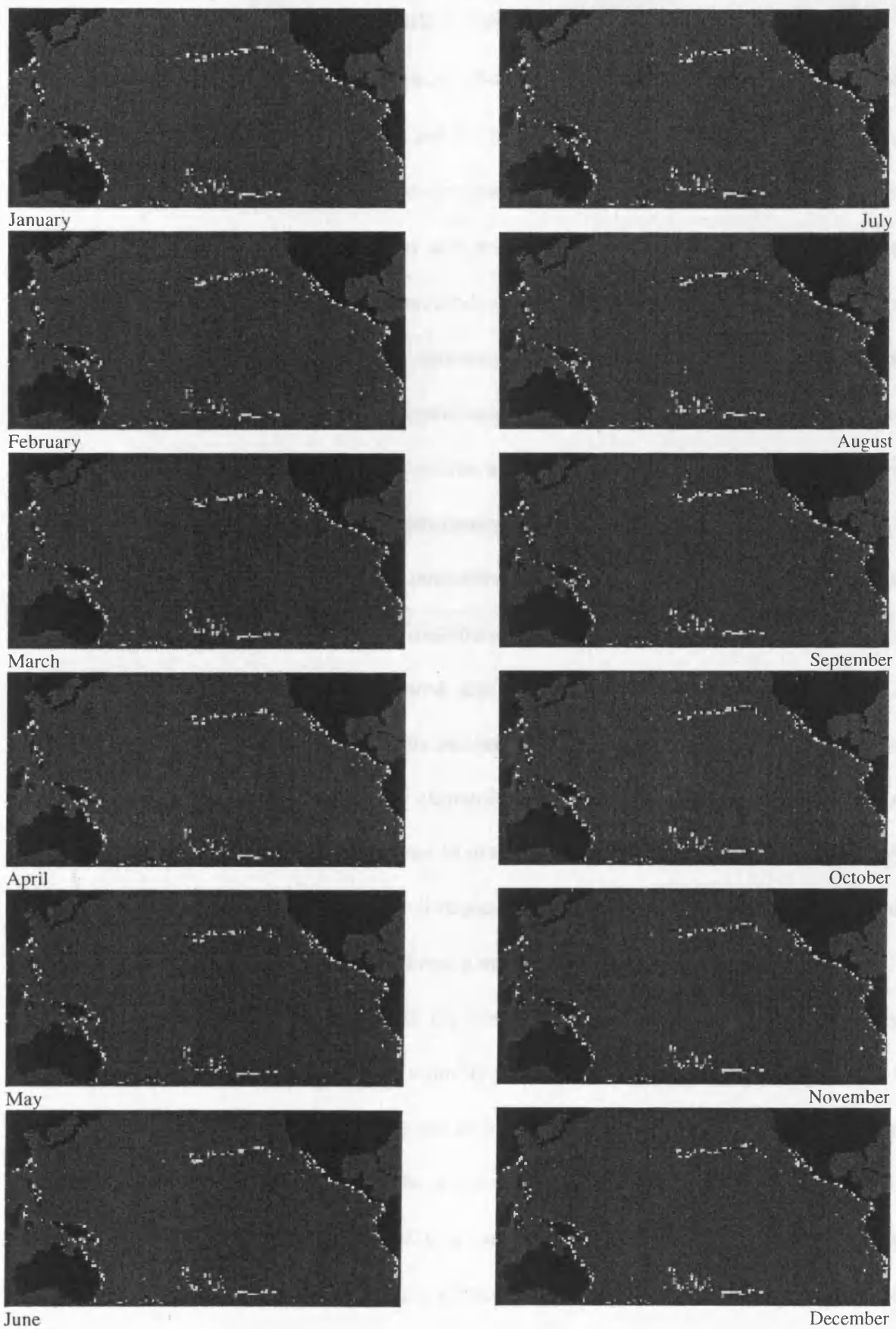
Fig. 5.3. Annual cycle for predicted concentrations of Skipjack tuna in the Pacific Ocean. Data for the first day of each month

5. DISCUSSION

The model is presented here as a proof-of-concept exercise. The concept that has been proved is that it is possible to build a model based on sound ecological principles that integrates ocean variability with fish movements in a non-prescriptive manner, and which uses the capabilities of satellite sensors and numerical ocean modelling to fill the gaps inevitably left by conventional sampling methods. Much work remains to be done before it or a model like it could be used with any measure of reliability in the management of tuna fisheries. Nonetheless it has been a successful scientific endeavour that shows great promise for future application. Here I discuss the results and point to some important components of the model that require attention in future laboratory, sea-going or computer-based research.

The results given in Fig. 5.3 are indicative of the potential of the model, rather than being a plausible prediction of skipjack distribution in the Pacific Ocean. The population is actually rather static, being concentrated around the perimeter of the Ocean and at tropical/sub-tropical frontal systems. This reflects 2 aspects of the model: firstly, the low variability inherent in the use of monthly climatological input data; and secondly, the lack of density-dependent feedback from predators to prey (i.e. there is no forage depletion by high concentrations of tunas, and no chlorophyll depletion by high concentrations of forage). This must be addressed in the future by the following means.

Most obviously, better input data are needed. The mean field is never (or rarely) experienced in the ocean and the use of monthly means also dampens the seasonal cycle. It has been previously shown that apparent spatial shifts in the Pacific skipjack population are linked to large zonal displacements of the western equatorial Pacific warm pool that occur during ENSO events (Lehodey et al. 1997). A longer time series of 'real' data (i.e. satellite observation and numerical simulation) for the Pacific ocean would provide a less predictable and therefore more challenging environment to which the model tuna must adapt. The results might then look more similar to observed skipjack distributions (cf Bertignac et al. 1998).

There are then two weak links in our knowledge, because they are the most difficult to derive by measurement or modelling yet the most important for survival and growth: these are the different components of natural mortality, with particular reference to early life history, and the spatio-temporal dynamics of tuna prey or forage distributions.

Previous work has investigated natural mortality of tuna larvae (Davis et al. 1991) but the different components have not been separately quantified. It is not a simple task to simultaneously quantify feeding success (see Fiksen et al. 1998, Fiksen & Folkvord 1999), and also predation risk (see Mullin 1993). Yet both mechanisms will operate to varying degrees and with different spatio-temporal extents. The separate mortality coefficients, calculated as described above under SUBROUTINE GROWTH, sum to give a total coefficient for natural mortality that is consistent with observed magnitudes. However, it would be more satisfying to use direct measurements of the independent mechanisms. If such data are obtained in the future then they can easily be incorporated in a model such as this.

Tunas are not thought to be selective feeders but rather their diet reflects the relative availability of different prey types. Schools of tuna feeding on oceanic anchovy *Encrasicholina punctifer* have been observed on several research cruises (Hida 1973, Ozawa & Tsukahara 1973). *E. punctifer* is primarily an offshore species and is broadly distributed throughout the Indo-Pacific region but is dominant in the surface waters of the tropical western Pacific (Ozawa & Tsukahara 1973). The species is a major prey item of juvenile and adult tuna (Hida 1973, Ozawa & Tsukahara 1973, Itano & Williams 1992, Buckley & Miller 1994, Itano 1999). Larval skipjack feed primarily on fish larvae, and *E. punctifer* larvae is a dominant component (Tanabe et al. 1999). An examination of gut contents of yellowfin tuna, including a high proportion of reproductively active females, found *E. punctifer* to be the dominant food item by frequency and volume (Itano 1999). This is not surprising, given the relatively high abundance and energy density of this prey fish, and considering the high energy requirements of frequent spawning (Schaefer 1998). The oceanic anchovy feeds primarily on copepods (Hida 1973). Zooplankton concentrations become rapidly decoupled

from chlorophyll concentrations in the surface ocean, simply due to their slower growth rates (Abraham 1997), which is why chlorophyll alone is a poor proxy for productivity at secondary and higher trophic levels. *E. punctifer* may provide a critical link between plankton productivity and the aggregation dynamics (for feeding and reproduction) and therefore the vulnerability to surface fisheries of larger pelagic fishes, such as skipjack and yellowfin tuna (Ozawa & Tsukahara 1973).

Modelling the spatio-temporal dynamics of tuna forage has been the focus of work by Patrick Lehodey at the Secretariat of the Pacific Community, New Caledonia (Lehodey et al. 1998). The results of the earlier simulations that have been used as input data here are no longer considered to be very reliable (P. Lehodey pers. comm.) but recent work is much improved, with the development of a 20 yr time series of forage concentration in mmolN m^{-3}. Future collaboration is planned, to input this new data to the model developed here. Given the importance of the oceanic anchovy to western Pacific tuna, further work might consider its life history strategy in a similar way to the model developed here for tuna, rather than the biogeochemical mass-balance approach that is presently being followed.

The conversion of forage concentration, whether input as an index or as an elemental mass (i.e. mmol N), to a prey concentration that is realistically 'packaged' is, at this stage, a somewhat creative exercise. The necessary conversion is from elemental mass to biomass, and then from biomass to the number of schools of any given mass. Direct measurements of tuna forage concentration have not as yet been possible (Roger 1994). Acoustic methods are likely to prove useful in this regard (e.g. McClatchie & Coombs submitted), particularly as they extend their abilities to discriminate size classes if not species of pelagic fish. The data required are attainable in principle, which justifies the use of forage index at this stage. The index can be replaced by better simulated data and/or observed data as it becomes available.

The model structure itself is adequate but there are various modifications that could be made in order to improve the realism of its formulation and potentially of its results. Most obviously, the two sexes could be separately represented. With different energetic

requirements it is possible that different life history strategies might emerge for males and females. However, for Pacific tunas in general, no divergence is seen in the spatial distributions of the sexes and males only grow slightly larger than females (Murray et al. 1999). The use of only one sex in the model tuna is therefore a justifiable simplification.

Models using ANNs can be quite sensitive to the structure of the network itself. This has not been investigated here and the network has been kept comparatively simple. It is possible to allow the structure of the network to also evolve in the course of the model run (Rechenberg 1994) although that may be more appropriate for applications that are working back from a predetermined solution i.e. fitting to data. This has not been the goal here but it might be worth exploring this topic, allowing different fish to evaluate different variables in different ways. Similarly, it is possible to use more than one network so that different decisions are evaluated separately (e.g. movement and spawning). This might also be investigated in future work.

5.6. CONCLUSIONS

This work is still at a comparatively early stage of development. Yet it is a highly original approach that might find important practical application as the model is improved. A better model would justify more rigorous testing against observations; at this stage it is quite obvious that the predicted fish distributions do not represent observed distributions very well. But the exercise has proved the point that it is possible to integrate behavioural models for fish with whole-ocean circulation and production models, and shows how the various aspects of biological detail (physiology, sensory biology, growth, movement, reproduction) can be brought together to represent the life-history of an evolving population over many generations. The model is reviewed in more detail in the final chapter, along with observational and other modelling studies for the behaviour of tunas in relation to their environment. The importance of this approach, particularly with regard to the use of satellite remote sensing in fisheries, is discussed and proposals for future research are detailed.

CHAPTER 6
DISUSSION & CONCLUSIONS

CONTENTS

6.1. SUMMARY

Modelling efforts that seek to describe, explain and predict the behaviour and spatial dynamics of tunas, including those presented in this thesis, are reviewed and discussed in relation to field studies with the same goals. Tagging and tracking of fish with electronic devices can provide valuable observations of free-living animals, which may be used to help derive models and also to test their predictions. But it will not be possible to derive and evaluate models for the fine-scale behaviour of tunas unless measurements are made of physiological and environmental variables, representing factors motivating behaviour, at the same time as position and activity are recorded. On longer time and space scales, reproductive motivation must be assessed, by identifying spawning grounds and times and measuring gonad state for individuals as they migrate throughout their range. Thermodynamics (through bioenergetics), fitness maximisation and adaptive behaviour with evolutionary motivation are appropriate paradigms for the derivation of models. But modelling will remain merely a technical exercise unless it is carried out as an integrated part of research programs pursuing the understanding of tuna behaviour and spatial dynamics as the ultimate goal. An observational framework that simultaneously measures environmental and physiological variables, with a complementary suite of statistical and theoretical models, will truly advance knowledge. This synthesis will only be achieved through collaboration between scientists with individual skills in field, laboratory and computational ecology and with innovative technical support. Satellite platforms will provide increasingly accurate measurements of surface ocean variables over large space scales and with rapid repeat sampling. The real challenge remains to relate these variables to habitat preferences of fish. Statistical methods incorporated within 'geographical information systems' (GIS) may have some utility in regions of low variability. For highly dynamic ocean environments with spatial and temporal heterogeneity in key variables, predictive models might have more success if they incorporate what we know of fish physiology, behaviour and life history characteristics — this thesis has reviewed and developed methods to support this.

6.2. FUTURE RESEARCH AND APPLICATIONS

6.2.1. Tuna behaviour: observations and modelling

6.2.1.1. Introduction

It has long been a goal of ecologists to fully describe the behaviour of tunas in relation to their oceanic environment. Large scale movements have received much attention because of the complexities surrounding the management of highly migratory stocks (Block et al. 1998a). Certainly these issues are important if seeking to apply traditional fisheries models for stock assessment and quota management. Mark and recapture methods have been used for various applications including large scale movements, growth rates, mortality, and transfer rates between stocks and gear types (see review by Hunter et al. 1986a). Acoustic telemetry has provided detailed data on tuna movements, often in relation to environmental variables measured from the recording platform (Holland et al. 1990, Cayré & Marsac 1993, Block et al. 1997, Josse et al. 1998, Brill et al. 1999, Dagorn et al. 2000). Archival tags have collected longer time series of data on position and water temperature, and sometimes body temperature (e.g. Block et al. 1998b), without the need for a following platform, but the need to recapture the fish before data can be obtained is clearly limiting. Pop-up tags that relay their data via satellite have been used to effectively increase the return rate to near 100% (Block et al. 1998a), but only position and daily mean water temperature have so far been recorded, limiting the utility of the results.

A common problem for all tagging studies to date is sample size; only a small number of fish may be tagged and tracked at any one time, and repeated sea-going experiments are costly. Biologists have not worried overly about this and for good reason — individual behaviour may be scaleable into populations and species as the same physiological and evolutionary imperatives apply to all. This doesn't negate the need to sample more than 1 fish at a time, but it does allow us to have confidence in good, comprehensive studies that have limited sampling size.

The common framework for understanding animal behaviour is behavioural ecology (Krebs et al. 1993, Krebs & Davies 1997). This is a unifying field that provides some powerful perspectives, paradigms and methods that can be applied across the animal kingdom. A conceptual model for the behavioural ecology of tunas is presented in Fig. 6.1. Theoretical models in behavioural ecology (e.g. Kirby et al. 2000, Chapter 4) need observations for parameterisation of vital rates and for testing predictions. In turn they may contribute to experimental design by identifying key variables and parameters. Statistical models based solely on observations and without regard to mechanism or process can say nothing about causal links between variables, but may still have pragmatic value and find useful applications (e.g. Cayré & Marsac 1993). In this chapter, differences in modelling methodologies are discussed and the common ground that can exist between observational and computational studies is emphasised. My contention is that we might learn so much more if we refine our observational methods and our modelling techniques to a point where they converge as valuable tools for the same task.
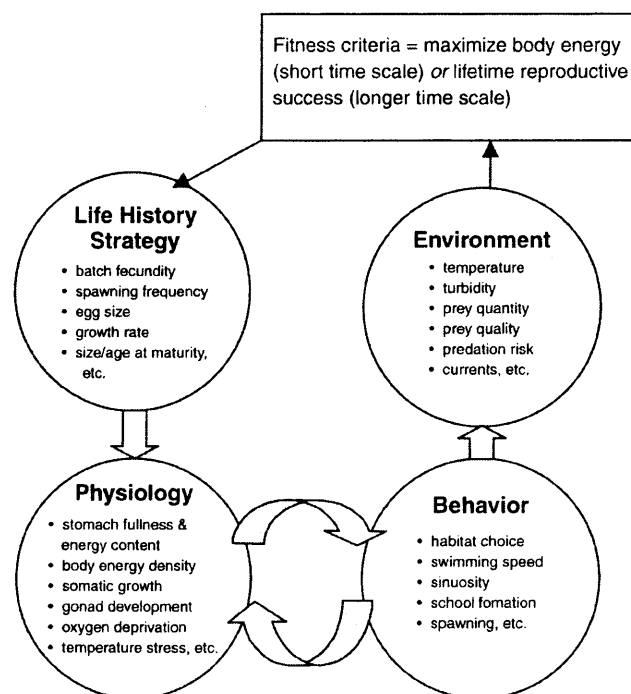
Fig. 6.1 Conceptual model for the behavioural ecology of tunas. The properties of the oceanic environment interact with physiological constraints and evolutionary imperatives. In order to maximise some measure of fitness, a predatory fish comes to optimise its use of available habitat, through natural selection against sub-optimal strategies, and by making cognitive choices within the constraints of its sensory and learning abilities

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6.2.1.2. Observations

Much observational work has focussed on the role of physical or abiotic aspects of the environment as potential limiting factors in horizontal and vertical range. Many physiological processes are temperature and/or oxygen limited, so this focus is understandable. Despite the mechanisms of heat conservation that are available to tunas (Kishinouye 1923, Carey & Lawson 1973, Holland et al. 1992, Dewar et al. 1994), temperature limitation of foraging range is suggested by laboratory experiment (Dizon et al. 1977, Barkley et al. 1978, Brill et al. 1998) and apparent in field observations (Blackburn 1965, Sund et al. 1981, Brill 1994a, Brill et al. 1999). Oxygen concentrations can be limiting in absolute terms, and even if they are not there may be clear preference for high oxygen depth strata (Block et al. 1997). Cayré & Marsac (1993) tagged and tracked 3 yellowfin tuna, recording depth every 20 s and comparing vertical movements with profiles of temperature and dissolved oxygen. They fit modified normal distributions to the time series of data such that a depth-based catchability forecast could be made and fishing gear set depending on observed profiles of the physical variables. However, their conclusion that '...the vertical distributions of only 2 physical parameters (temperature and dissolved oxygen) explain the vertical distribution of yellowfin tuna' is somewhat exaggerated, particularly as they did not postulate any reason for the observed distributions, nor did they measure other potentially relevant variables such as light and/or turbidity. A statistical model of this nature may become a useful means of directing fishing effort but it does not advance our understanding of tuna behaviour. In the light of various experiments noting the dynamics of tuna prey (Marchal et al. 1993, Josse et al. 1998), conclusions constraining tuna behaviour by physical variables alone would seem overly simplistic. Even if we assume that adult tunas are apex predators and that their behaviour is not at all constrained by predation pressure, their behaviour is highly likely to be affected by the dynamics of their highly mobile and patchily distributed prey.

Tunas are known to have high metabolic energy demands (Brill 1987, Chapter 3) which necessitate a high energy intake. Given the need for tunas to keep swimming in order

to maintain hydrostatic equilibrium (Magnuson 1973), we might expect active foraging to occur whenever possible. However, it has been noted that the intensity of response of yellowfin tuna to prey odours varies with hunger state (Atema et al. 1980); time is needed to recover from exercise and to digest and absorb food. Energy conserving 'dive and glide' behaviour has also been observed in more than 1 tuna species (Holland et al. 1990, Block et al. 1997), whereby rapid powered ascents are followed by a slow, lift-based glide. Both time- and state- dependent behaviour are predicted theoretically (Chapter 4, Kirby et al. 2000), which means that unless environmental and physiological variables are simultaneously measured, it is simply not possible to say what is controlling tuna behaviour.

Josse et al. (1998) acoustically tagged and tracked 1 yellowfin and 2 bigeye tuna, and simultaneously measured local prey density as indicated by a sound-scattering layer (SSL) on an echosounder. They obtained some good data illustrating the movements of these fish in relation to the SSL and noted that abiotic variables (temperature and oxygen) were not limiting. It is rather telling that they are able to conclude that they have observed a '...new (sic) explanatory factor of tuna behaviour: the biotic environment.' It is new but it shouldn't be — as pelagic predators, tunas are ever likely to be affected by the dynamics of their prey. There has been too much focus on the relationship of tunas with physical environmental variables. These abiotic variables are still important for tunas and there may be real situations where they are limiting, but within the limits of these variables that directly affect physiological processes, it has long been recognised that the availability of forage will induce tuna distribution (Blackburn 1965, Sund et al. 1981).

Fine scale hunting behaviour is therefore also likely to be observed. Vertical movements in particular are common and frequent and the different tunas have different movement patterns. The reasons why these differences occur remain the subject of debate (Brill et al. 1999) and morphological and/or biochemical adaptation to the different physical regimes above and below the thermocline are likely to be key (Lowe et al. 2000).

The evolutionary advantage of these different behaviour patterns requires more holistic consideration of the trophic dynamics of the pelagic ecosystem. Trophic interactions are not just important for fine scale behaviour; even large scale movements and aggregations may be food-motivated. The gathering of young albacore at the fronts off the California upwelling is a case in point (Laurs et al. 1984, Fielder & Bernard 1987) — being sexually immature, these fish are not aggregating for reproduction. Assuming that tunas can occupy a broad oceanic niche, the proximate motivation for their dynamics within that space is likely to be food, with the ultimate motivation being to maximise reproductive success. Behavioural studies should therefore focus on estimating these factors as the free-living tuna is observed.

6.2.1.3 Modelling

Biologists are often put off by the 'flute music' of calculus, the sophistry of statistics and the terse logic of programming code. When one's motivation for study comes from a deep appreciation of the beauty of nature it is easy to be put off by analytical methods that seem to grossly oversimplify or overcomplicate, sometimes simultaneously, a situation about which one already has an intuitive understanding. But such is the nature of science, and modelling is but another tool in the investigation of natural processes, and one that can contribute to knowledge at many different levels of understanding. While stock assessment may have '...degraded into mathematical games in which the object is to find best guesses and estimates for parameters that have little to do with any 'real' measured or measurable variables' (Sharp 1995) the exercise of deriving a model can still help to identify/clarify the relative importance of different parameters and processes. Simpler models often provide insight that is more valuable than accurate numerical fits, and the most influential models often do not need the numerical output to guide the qualitative understanding (Hilborn & Mangel 1997).

Herein lies the truth that there are many different types of model that may be applied to any particular question. For practical application it is often desirable to be able to predict a property that is difficult/expensive to measure from another that is easier/cheaper to measure. If such correlations are lagged then we have an empirical means of forecasting. There are

some successful examples of this work in remote sensing and fisheries (e.g. Waluda et al. 1999) but in general it is extremely difficult to find statistical relationships that hold in highly variable environments (Sharp 1995, Mangel et al. 2000; and see Bigelow et al. 1999, Andrade & Garcia 1999). Furthermore, as discussed earlier (Chapter 1), while statistical relationships may describe relationships well or badly, they cannot be used to show causality (Sharp 1995, Brill 1997, Hilborn & Mangel 1997). We may use statistical methods to identify relationships between variables but the ultimate questions regarding why such relationships exist cannot be answered in this way. Causality may be established through knowledge of specific obligate physiological responses and consequent behavioural decisions in a systems context (Sharp 1995, Kirby et al. 2000, Chapters 4 & 5, Fig. 6.1). This theoretical approach has its emphasis on identifying mechanisms of interaction between organism and environment, allowing cause and effect relationships to be established and used to make predictions that may be better founded than those based on projection of past trends into the future. The level of detail required to develop such process-oriented models is usually high, and simplifications and assumptions have to be made in order to progress. Nevertheless, even simple theoretical models that forgo mechanistic detail can still provide a better understanding of the system under study than may be obtained by statistical analyses alone, as they can also have explanatory power. Of course, 'understanding' in the sense of knowing causal mechanisms, may be quite different from successful prediction, and society is often more interested in the latter. An ultimate aim of this thesis is to show that detailed understanding may provide a better basis for predictions; I acknowledge that this is 'not proven' (yet).

Models for the behaviour and spatial dynamics of tunas are many and varied (Deriso et al. 1991, Cayré & Marsac 1993, Dagorn et al. 1995, 1997, Bertignac et al. 1998, Dagorn & Freon 1999, Sibert et al. 1999, Stöcker 1999, Humston et al. 2000, Kirby et al. 2000, Chapters 4 & 5). Rule-based methods have been used to investigate both fine-scale behaviour of tunas (Dagorn et al. 1995, Dagorn & Fréon 1999) and larger-scale movements (Dagorn et al. 1997, Humston et al. 2000). The use of 'rules' is a prescriptive exercise and so the rules themselves

must be simple, logical and defensible. Complex behaviour and spatial dynamics may then emerge in the model system that allows one to generate and evaluate hypotheses for real tuna. Large scale movements and population dynamics have been represented by advection-diffusion relations, with tagging data used either in model derivation (Sibert et al. 1999) and/or evaluation (Bertignac et al. 1998, Sibert et al. 1999). Models of this type and at this scale ignore more fine-scale behaviour but may still incorporate interactions with environmental variability e.g. SST and forage density (Bertignac et al. 1998).

The model of Bertignac et al. (1998) for the spatial population dynamics of Pacific skipack tuna *Katsuwonus pelamis* builds on earlier levels of modelling, covering general circulation (Blanke & Delecluse 1993), biogeochemistry and new production (Stoens et al. 1998), and tuna forage production (Lehodey et al. 1998). In this way the model as a whole is prognostic for tuna. It is a bold attempt at modelling spatial population dynamics from a 'bottom-up' approach (i.e. from first principles — physics to fish) and is commendable in its endeavours to link biological oceanography with fisheries science. However, the use of differential equations implies that one has already identified the relevant dynamics and, in the case of fish movement models, the relationship between fish and environment (Eqs. 4, 9 & 10 in Bertignac et al. 1998). Given the complexities of ecological interactions, and the different components of fitness that trade-off against each other in the course of an animal's lifetime, this may be somewhat premature. A similar criticism would apply to the kinesis model of Humston et al. (2000) and, in fairness, to mathematical ecology in general. One can apply mathematical models of any particular functional form to any postulated relationship between variables, but there should be good justification for the choices made. Particular caution should also be exercised in the inferences drawn from the results. Humston et al. (2000) are successful in their aim to reproduce large-scale migration of Atlantic bluefin tuna from simple behavioural rules. These movement rules are formulated mathematically as functions that depend on the difference between actual and optimal temperature, the latter (18°C) being, '...chosen because it concurs with temperature data for those tuna,' aerial survey data

reported by Lutcavage et al. (1997), and because '...it is linked to the edge of Gulf Stream waters.' In the absence of any other factors to trade off against this temperature preference it is then no surprise that the resulting distributions reflect those data used to derive the function, such that '...histograms of surface temperatures occupied at the end of model runs indicate highest concentrations of fish in surface waters of 18°C,' and model results 'also showed marked aggregations along the edges of sharp thermal fronts.' This is skating on thin ice, below which lie the frigid waters of tautology. The model is attractive in its simplicity and forecasting skill, and in the aim to reflect observations the authors succeed admirably. But the assumptions made concern the mechanisms of interaction between fish and environment, as well as the motivations for action, upon which there is not yet convincing consensus. This is an area where future experimental research will be key.

It is well to remember that '...the realism of spatially resolved models cannot evolve faster than the acquisition of knowledge about the mechanisms governing the spatial behaviour of the constituents' (SERG 2000). The level of realism that is incorporated into a model will also depend on its purpose and intended use. In the optimal foraging model (Kirby et al. 2000, Chapter 4), where the aim was to be as true to mechanism and motivation as possible, it was not possible to simulate tuna behaviour unless a detailed representation of physiology (gastric evacuation, standard and active metabolic energy costs; Chapter 3), sensory systems (visual range; Chapter 3), and both biotic and abiotic characteristics of the environment (prey abundance and energy density, water temperature and turbidity; Chapter 4) were included. I faced the same task as Bertignac et al. (1998) in trying to derive an equation to represent the effect of temperature stress on tuna, a task where we are totally dependent on experimental physiology to give us measurements of vital rates. By specifying a range of acceptable behaviours (swimming speeds and habitats) and a detailed representation of the state dynamics (i.e. physiology) the modelling technique calculates fitness values for all possible solutions and predicts optimal foraging behaviour (for more detail see Mangel & Clark 1988, Clark & Mangel 2000, Kirby et al. 2000, Chapters 3 & 4). The exercise began

with the aim of deriving a means to predict the location of tunas in relation to ocean fronts visible in satellite imagery. But these data are of physical variables only, with the exception of chlorophyll concentration, and the importance of prey characteristics and state dependent behaviour became obvious only in the course of literature searching and model derivation and evaluation. Nonetheless, I succeeded in predicting behaviour from physiology in a complex environment, and inadvertently developed the optimal foraging model envisaged by Hunter et al. (1986a, p 30). The model still contains assumptions that may or may not be true, because our knowledge of various components is incomplete (e.g. sensory biology of tunas; physiological mechanisms and rates of accumulation of thermal stress; optical and nutritional properties of forage), but it is the first model for tunas that predicts behaviour from physiology and environment; this kind of model is most closely related to tagging studies that seek to understand fine-scale behaviour.

For movements over larger time- and space-scales, if a mechanistic representation of reality is desired, a different approach again may be necessary. There are real issues regarding the scaling up of motivated individuals to the dynamics of populations but these may not be as formidable as they first seem. Using evolutionary motivation (i.e. some measure of reproductive success) spatial population dynamics has been modelled by both optimisation (Fiksen et al. 1995) and adaptation (Huse & Giske 1998) approaches (see Giske et al. 1998 for expansion and discussion of these terms). Adaptive models are well founded in evolutionary and life-history theory, and use computational methods inspired by biological processes (i.e. neural networks and genetic algorithms), which enable model agents to both learn and evolve just as with living creatures. They are also well suited to complex solution space (G. Huse, pers comm.) and may therefore be better suited to exploratory simulations of the effects of changes in exploitation patterns or ocean climate on fish population dynamics. This heuristic or 'black box' approach has its detractors, usually amongst those more familiar with deterministic rather than adaptive processes, but it is conceptually satisfying to the biologist who is well aware of the complexities of living creatures and to whom adaptive behaviour and

evolution are far from alien. The development of an adaptive model for the spatial dynamics of Pacific skipjack tuna is the subject of my current research, with progress to date presented in Chapter 5. Further development of this model should be followed by comparison with different approaches to the problem (Sibert et al. 1999, Bertignac et al. 1998).

6.2.1.4. A combined approach

One of the greatest contributions that theoretical modelling can make in studies of behaviour is that various hypotheses can be jointly evaluated and refined, prior to field observation and statistical hypothesis testing. The use of models when planning an experiment may also help identify variables that may be confounded in the analysis of results (Hilborn & Mangel 1997). This combined approach has practical as well as intellectual merit, as computational experiments are comparatively cheap to run, and may then allow field studies to focus on what is really important for enhancing understanding. This is the essential point that I want to press in this chapter, with regard to the complementary roles of modelling and experimental studies of the behaviour of tunas in relation to their environment. Observations should be used to derive and evaluate models, which in turn may be used to guide investigations in the field through the generation of testable hypotheses. As already mentioned, in the optimal foraging model (Kirby et al. 2000, Chapter 4) it was necessary to include a detailed representation of environmental characteristics, prey characteristics, sensory systems and physiology in order to predict optimal habitat and swimming speed. Such detail can only come from experimental investigation in the laboratory and at sea. The model also makes predictions, in particular regarding state-dependent behaviour, for which comparable observations are not yet available. I hope that in the future, researchers will adopt the model, or at least the approach, and use it to guide their investigations.

Joseph & Wild (1984), summarising a meeting of the Inter-American Tropical Tuna Commission, noted that '...there is a need to organise more complete conceptual models on how environmental conditions and physiology can direct and limit tuna movements both vertically and horizontally...At-sea tagging operations should be accompanied by sampling to

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determine physiological state (energy storage, instantaneous growth rate, etc.) and recent reproductive history. Tuna stomachs can be used to monitor and assess the environment in terms of temporal and spatial food availability.' From the literature it seems that this advice has not been taken. There are separate studies that tag fish and others that measure stomach contents but few that do both, let alone conduct the other physiological investigations suggested. In some areas, techniques should have progressed such that we can identify forage fish by acoustic target strength. There may also be ways of non-destructively measuring hunger state through the use of chemical sensors on the fish. This would be vital information for a physiology-based movement model, data that might be recorded by archival tag along with swimming speed and sinuousity. I made an assumption earlier that adult tunas are apex predators and are not themselves preyed upon. This is generally thought to be the case, but as Hampton (2000) has shown, natural mortality of small (21–30 cm) skipjack, yellowfin and bigeye tuna is an order of magnitude higher than that of mid-sized fish. To understand the behaviour of these fish we must then simultaneously measure or otherwise estimate predation risk for the environment where our tuna is under study. I am not aware of tagging methods that will record the presence of other fish, be they predators, prey or conspecifics, but it would be worthwhile considering how they might be developed, or at least how we might simultaneously measure the 'biotic environment' (e.g. Josse et al. 1998) in terms of both predators and prey. 'The time and space scales of measurements of tuna movements is a critical issue in the design of future investigations. Tracking of individual fish over periods of hours or days is not equivalent to movements of groups or schools over months. The problem of using information from small-scale movements to model movements of large groups of tunas over weeks or months needs to be examined' (Joseph & Wild 1984). Different models may be used to investigate these different aspects of movement. An optimal foraging model (e.g,. Kirby et al. 2000, Chapter 4) is a good paradigm for short time-scale behaviour but is not adequate for scales where motivation is different i.e. where reproductive activity must be considered. In this case, a fitness measure that is more directly linked to reproductive success

must be adopted (e.g. number of eggs laid per gram body mass above size at maturity —

Fiksen et al. 1995, Fig. 6.1) or the concept of 'endogenous fitness' can be applied. Either an

optimisation or an adaptation approach can be used (Giske et al. 1998). An adaptive model

applying the concept of endogenous fitness has been presented here (Chapter 5) as a 'proof of

concept' exercise; further work will extend its application over a multi-year time series of

observed/simulated data.

There are technological and logistical obstacles and constraints in the observational

work suggested, and first we need to clarify which variables are most relevant to behaviour.

Indices, proxies and vital rates for these variables may be identified in the laboratory, and

then the technological development of new tools can begin. Modelling methods must be

scrutinised, with methods used that are appropriate to the questions asked. Statistical models

must not pretend to tell us why things happen, and theoretical models must be explicit in their

assumptions and expand their scope from the artificial environments for which they are

originally derived. Tremendous progress has been made in the physiological ecology of tunas,

and in the development of computational methods; these fields must converge and be

followed by behavioural and evolutionary studies that go beyond the descriptive and

retrospective, and are focussed on understanding and prediction.

6.2.2. Geographical information systems (GIS)

A Geographical Information System (GIS) comprises of a collection of integrated

computer hardware and software which together is used for inputting, storing, manipulating,

analysing and presenting geographical data (Meaden & Do Chi 1996). Some authors include

the requirement for trained staff to the definition of a GIS and others add that its primary role

is to aid decision making; different researchers, policy analysts and decision makers will have

different requirements and will obviously develop systems accordingly. Applications of GIS

in fisheries research can be seen in the UNESCO publication to which I have contributed a

chapter (Kirby in press) and in the proceedings of the 'First International Symposium on GIS

in Fishery Sciences' held from 2–4 March 1999 in Seattle (Nishida et al. 2001), with

examples of biological research and statistical modelling as well as fisheries management. Many of the case studies presented utilise remotely sensed data and statistical modelling. The success or otherwise of a marine fisheries GIS will be determined by the extent to which the relevant data can be collected, co-located and displayed in such a way as to enhance understanding. GIS generally allow user-friendly display of co-registered spatial data. However, further analysis is often required before relationships between variables can be established. This may be possible within a GIS but until recently the capacity of commercial GIS software for complex statistical analysis has been limited. This situation is changing as additional modules for spatial statistical analysis and/or dynamic modelling are being created, often by outside research groups. GIS-type software created 'in-house' will obviously be as simple or as sophisticated as its programmers allow. At the National Institute of Water and Atmospheric Research (NIWA), New Zealand, systems originally developed for the analysis of meteorological data and numerical weather prediction have been extended for SST and SSH data analysis, and are presently being used in the development of models for fisheries forecasting. The work presented in Chapter 2 was carried out using this system. Having been developed and presently running on a VAX VMS cluster, the user interface is somewhat non-intuitive, an important but neglected issue in the training and development of competent staff to fulfil the human component of a GIS. But the 'back end' represents a formidable suite of analytical tools and archived data. Future development, perhaps by using a web browser, might enable less skilled users to make better use of this resource. This is standard practice for repositories of large data sets (e.g. the World Ocean Atlas, Levitus & Boyer 1994).

Researchers who have been evaluating spatially resolved data for many years (e.g. meteorologists & oceanographers) do not consider GIS to be a particularly unique concept. The emphasis on data display rather than analysis in GIS has contributed to this impression. The collocation of data is a necessary precursor to modelling dynamic interactions, whether physical or ecological. The spatial life history model (Chapter 5) could be considered a GIS except that the emphasis is less on data display than on the underlying ecology. But while the

data display is somewhat crude but is considerably more advanced than that used in the optimal foraging model (Chapter 4). The use of computer animations in the presentation of oceanographic data and simulations presents a powerful impression of the underlying dynamics. Building such an interface to an active archive of data is an even more powerful tool for the researcher and may make data mining more intuitive.

6.2.3. Satellite remote sensing

The different geophysical variables measurable from space have been described earlier (Chapter 1). The emphasis of this thesis has been on trying to relate such variables to the dynamics of pelagic fish in a meaningful way i.e. by considering what mechanisms connect one variable to another. There has been much emphasis on trying to establish instantaneous correlations between satellite data and the relative abundance of fish and in some cases it has been possible to delimit favourable habitat. But the links between physics and fish operate across various spatio-temporal scales. The best example of this is in the potential use of satellite wind speed. There may be an instantaneous effect of wind speed on fish distributions; it has been reported that longline CPUE is higher when the sea is rough, the suggested explanation being that enhanced movement of baited hooks increases the encounter rate with predators and hence the 'catchability' of the gear (Kawamura et al. 1991). But the connection between wind speed and fish may also be more important much earlier on. Turbulence in the water column varies with the cube of the wind speed and fish feeding success varies with turbulence, particularly in the case of larvae (Fiksen et al. 1998). From this mechanism derives the 'optimal environmental window' hypothesis (Cury & Roy 1989), suggesting that pelagic fish recruitment, at least in upwelling areas, may be directly related to the overlying wind field in preceding months. Another example of the use of satellite-derived wind fields is in Chapter 5; the ocean general circulation model (OGCM) is driven by winds measured by ERS-1. The connection with the fish is firstly through the current field experienced, which is more important for larvae, but the OGCM also drives the biogeochemical model and hence the forage production, so there is a direct link through to the adults.

Sea surface height (SSH) is another variable that in itself would seem irrelevant to fish. But if SSH is used to derive geostrophic currents and their convergence/divergence is calculated we can map surface oceanographic features that might be attractive to tunas, through the enhancement of productivity which we assume is taking place there. The logic is again rather long-winded and SSH itself is merely a proxy variable for what is more relevant to tuna i.e. forage distribution. But features are identified in this way (Fig. 1.11) and SSH can also be used for investigations of larval drift (e.g. Polovina 1999, Chiswell & Booth 1999).

Sea surface temperature (SST) is the most common data type referred to in fisheries applications of satellite remote sensing. Again the emphasis has been on feature identification, so again the variable itself is largely a proxy for assumed higher production in convergence and upwelling zones. As I have illustrated in this thesis (Chapter 4) the link between SST features and fish distribution is not straightforward and other researchers have shown that predator and prey concentrations are not necessarily any higher in fronts or related features compared to surrounding waters (Power & May 1991, McClatchie & Coombs submitted). Temperature is very important for the physiological ecology of fish but tunas are highly adapted to mitigate its effects. Habitat preferences may be apparent and shifts in water mass distribution may cause shifts in the distribution of fish. The mean and variability of SST can be determined, and running mean and anomaly data can be used to evaluate present conditions. Preferred temperatures for adult fish must be determined but this can delimit such a large area of ocean as to be useless for directing fishing effort. Different life history stages may be more vulnerable to the effects of temperature stress than others. Adult albacore for example, are found in surface waters north and south of the equator but in deeper, cooler waters at the equator itself (Blackburn 1965, Sund et al. 1981, Murray et al. 1999). By modifying their behaviour they can adapt to that particular environment, with obvious effects on the efficiency of surface fishing gear. The effects of temperature stress on eggs and larvae may be more critical and larvae are not likely to survive in waters that are too hot or too cold. This is apparent in the seasonal distribution of yellowfin tuna larvae (Itano 1999).

6.2.4. Spatial modelling

The major part of this thesis has been concerned with the derivation of models connecting the behaviour and distribution of fish with the ocean environment. Satellite platforms enable measurement of geophysical variables over large areas but, as outlined at various stages above, it is my opinion that these data must be assimilated into detailed ecological models in order to fully exploit their potential. These models do not already exist, so they must be created. My work in Chapter 5 and the work of others (e.g. Fiksen et al. 1995, Huse & Giske 1998, Lehodey et al. 1998, Bertignac et al. 1998) are among the first attempts at such a synthesis. Much work has been done in the modelling of ocean circulation, which in itself may be important for the maintenance of populations, through nutrient enrichment and the transport and retention of larvae (Bakun 1996). The general consensus in this field is that ocean models cannot get much better except through improving the quality of the data assimilated into them (M.J. Uddstrom pers. comm.). This is not the case in ecological studies, where we still strive to understand pattern and process and to identify appropriate levels of detail for model building. The major efforts to date have used advection-diffusion-reaction models (Lehodey et al. 1998, Bertignac et al. 1998, Sibert et al. 1999) yet these are prescriptive and without regard to mechanism. The model framework developed here (Chapter 5) incorporates far more biological detail than these other models, representing the effect of each environmental variable directly and does not presume to know how the various factors trade off against each other. The model allows behaviour to evolve as an adaptive response to proximate conditions over successive generations. As the model is developed further, various aspects of fish life history could then be investigated, such as the spatial distribution of the different components of natural mortality, and the evolution of migration strategies and/or subpopulations.

6.3. RESEARCH PROPOSALS

Research proposals have been submitted to agencies in Europe and New Zealand; with ongoing collaboration, this thesis should provide a sound basis for development in this field.

6.3.1 Discussion paper submitted to New Zealand Ministry of Fisheries

CPUE for tunas within the New Zealand EEZ is neither randomly nor uniformly distributed in space; this much is obvious as fishers have come to target their effort at particular areas. Within the smaller sample space of observed fishing sets, frequency distributions of CPUE show that it is still an over-dispersed quantity (i.e. variance is greater than the mean). This implies that the prior knowledge of fishers is still not perfect. Even non-schooling adult fish have been shown to be spatially aggregated at the sub-mesoscale level (<100 km). Ongoing work will investigate the relationship between such aggregations and oceanographic processes. What is also needed is to investigate the spatial properties apparent in the observed catch data in terms that relate more directly to the ecology of the target species. The assumption underlying this suggestion is that better understanding of the ecology of these species will enable more efficient fishing and facilitate an ecosystem approach to fisheries management as required by the Fisheries Act 1996. Attention to these factors is warranted by the fact that the target species are highly migratory and enter or pass through the EEZ as part of their larger scale movements. Variations in local relative abundance are therefore the immediate focus of interest for NZ tuna fisheries.

The research proposed falls under 3 separate but related categories:

1. sensory biology;

2. trophic ecology;

3. spatial dynamics.

The sensory systems of tunas determine how they interact with their environment, and the rate of biomass transfer through successive trophic levels is largely determined by the efficiency of these systems, coupled with food availability. There are major gaps in our understanding of the sensory biology of tunas (see Chapter 3). In turn, our knowledge of the trophic ecology of tunas (i.e. interactions with other species that govern the flow of energy and biomass through the system) specifically within the EEZ, is poor. This undermines further study on larger-scale fishery related problems, which form the substance of the third component — understanding movements of tunas within the EEZ. We know that areas of high/low CPUE change in the course of the fishing year but we cannot say, even diagnostically, what is happening when, where and why, because we have not undertaken robust studies that look at movements and the factors motivating movements within the EEZ.

To address some of these gaps, a combination of field and laboratory research, perhaps undertaken in collaboration with other Pacific nations, is proposed. Experiments to consider the availability of natural forage and fishing baits to tunas would address some fundamental gaps in our knowledge of tuna biology. Traditional and newly developed methods for studying trophic interactions in marine systems (stomach contents and stable isotope analyses respectively) could be deployed in areas that are known to be attractive to tunas, and the deployment of new tagging technologies would allow tuna movements to be observed directly. This, coupled with reanalysis of historical fine-scale catch data would result in a greater understanding of the ecology of tunas in the New Zealand EEZ, which would result in improved fishing efficiency and better informed resource management.

6.3.2 Proposal submitted to European Space Agency

ID 151
Title
MULTI-SENSOR SATELLITE OCEANOGRAPHY FOR PREDICTIVE FISHERIES
FORECASTING

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Executive Summary   The aim of this proposal is to develop and extend new methods in data synthesis and simulation in the field of multi-sensor satellite oceanography for operational fisheries forecasting. Our group has expertise in the synergistic use of satellite data coupled to models of physical oceanographic and marine ecological processes. We are presently developing new methods of modelling fish migration with the aim of coupling spatially explicit: individual based neural network genetic algorithm(ING)models with models of ocean dynamics and nearreal time data from satellite sensors. This proposal seeks to extend that work through the synergistic use of sensors aboard ENVISAT and would complement our plans to develop the modelling methodologies further by providing sufficient data for assimilation and validation, enabling the development of near-real time capabilities for fisheries forecasting.

Schedule   Since Jan 1997 and until Jan 2000 we have been and will continue to be working on the theoretical aspects of this topic, trying to understand and simulate the spatial dynamics of fish in relation to oceanographic features. This work is enabled by the studentship held by DSK under the supervision of PJBH and DLJ. From Jan 2000 until the launch of ENVISAT we would continue this work and prepare to assimilate the remotely sensed data into the models. From the launch onwards we would be ready to receive data and run our models, providing predictions of fish movements which will be testable by potential end users or by comparison with fish catch returns.

6.4. CONCLUSIONS

Fish biology (including physiological, behavioural and evolutionary ecology), physical oceanography, remote sensing and computer programming exist as disparate disciplines only in the social construction of science. In nature, fish live, reproduce and die within the self-organising complex adaptive system that is life on Earth. It is human minds that must remain open and human endeavour that must try to grasp what is useful and important from different scientific traditions in order to progress and deepen our understanding of life.

My thesis is that it is possible to model the dynamics of individual fish and fish populations in the oceans, in a spatially explicit context, by utilising the geophysical data obtained from space-based platforms, incorporated into models that couple physical oceanography and fish behaviour. The links between fish and environment (e.g. visual range, olfaction, temperature stress, larval drift) can be understood and represented in a quantifiable and integrated way. Behavioural patterns can be extracted from time series of fish catch data.

It is hard to conceive of methods for bringing together relevant information from different disciplines and/or aspects of the same discipline. In this work I have provided examples of how such a synthesis can be achieved. I have thoroughly reviewed, brought together and built on present knowledge. I have analysed surface longline data in an innovative way and I have developed and applied analytical and computational models in support of my thesis. I have illustrated how progress can be made in tuna ecology and in the application of satellite remote sensing to fisheries. Dedicated laboratory and sea-going research will be better focussed if they are conducted after prior identification of important data gaps and within a framework of analytical and computational modelling that is sensitive to and tries to incorporate the real complexity of nature.

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```
!   Inputs data supplied by Patrick Lehodey,
!   converts CZCS colour value to chlorophyll,
!   flags land & cloud,
!   scales Forage Index between 0-1
!   interpolates for missing value between Australia & PNG
!   outputs to formatted *.dat files for ING model, and *.txt files for animation
!
!   NB: if working from the self-extracting files provided, remove 3 alphabetic
! characters from cl_mthly_chlo.txt before attempting to run this program.

          implicit none

!  Declare variables

          REAL              land,cloud,maxF
          REAL              sum_t,sum_c
          REAL              sst    (180,1080)
          REAL              forage(180,1080)
          REAL              chloro(180,1080)
          REAL              u_comp(180,1080)
          REAL              v_comp(180,1080)
          REAL              temp(8),cphyll(8)

          INTEGER     iloop,jloop,kloop,count1,count2,a,b

          PARAMETER (land  = -8.)
          PARAMETER (cloud = -9.)
          PARAMETER (maxF  = 1.0)

          count1 = 0
          count2 = 0

          sum_t        = 0.
          sum_c        = 0.

!  Open input files

          OPEN(10,FILE='cl_mthly_sst.txt')
          OPEN(11,FILE='cl_mthly_F.txt')
          OPEN(12,FILE='cl_mthly_chlo.txt')
          OPEN(13,FILE='cl_mthly_u_opa7.txt')
          OPEN(14,FILE='cl_mthly_v_opa7.txt')
```

```fortran
!  Open output data files for SKIPJACK movement model

        OPEN(20,FILE='sst.dat')
        OPEN(21,FILE='forage.dat')
        OPEN(22,FILE='chloro.dat')
        OPEN(23,FILE='u_comp.dat')
        OPEN(24,FILE='v_comp.dat')

        OPEN(25,FILE='cloud.dat')
        OPEN(26,FILE='missing.dat')

!  Open output data files for RV ANIMATOR

        OPEN(30,FILE='AN_sst.txt')
        OPEN(31,FILE='AN_forage.txt')
        OPEN(32,FILE='AN_chloro.txt')
        OPEN(33,FILE='AN_u_comp.txt')
        OPEN(34,FILE='AN_v_comp.txt')

!  Read SPC data

      DO iloop = 1,1080

          READ(10,*)     sst    (:,iloop)
          READ(11,*)     forage(:,iloop)
          READ(12,*)     chloro(:,iloop)
          READ(13,*)     u_comp(:,iloop)
          READ(14,*)     v_comp(:,iloop)

      ENDDO

      WRITE (*,*) 'Input files read - now flagging land & missing values'
        !PAUSE

!  Flag land & cloud values - convert CV to cphyll

       DO iloop = 1,180
         DO jloop = 1,1080

           forage(iloop,jloop)= max(0.,min(forage(iloop,jloop),maxF))
           !limits F to between 0-1

           IF (sst(iloop,jloop).LE.0) THEN
```

```
              sst(iloop,jloop)   = land
              chloro(iloop,jloop)= land
              forage(iloop,jloop)= land
              u_comp(iloop,jloop)= 0.
              v_comp(iloop,jloop)= 0.

      ELSEIF ((sst(iloop,jloop).GT.0).AND.(chloro(iloop,jloop).EQ.255)) THEN
              WRITE (25,*) iloop,jloop,sst(iloop,jloop),chloro(iloop,jloop)
              chloro(iloop,jloop)= cloud
      ELSE
              chloro(iloop,jloop)= 10**(0.012*chloro(iloop,jloop)-1.4)
              IF (chloro(iloop,jloop).LT.0.) THEN
              Print *, "Negative Cphyll:",iloop,jloop,chloro(iloop,jloop)
              pause
              ENDIF
        END IF

    ENDDO
ENDDO

!make a channel between Australia & Papua New Guinea
DO iloop = 0,11
    a = 62+iloop*90
    sst(33,a)    = (sst   (32,a) + sst   (34,a))/2.
    chloro(33,a) = (chloro(32,a) + chloro(34,a))/2.
    forage(33,a) = (chloro(32,a) + chloro(34,a))/2.
    u_comp(33,a) = (chloro(32,a) + chloro(34,a))/2.
    v_comp(33,a) = (chloro(32,a) + chloro(34,a))/2.

      !& plug up the Panama Canal...
      b = 42+iloop*90
      print*,b,sst(171,b)
      sst(171,b)    = land
    print*,b,sst(171,b)
      chloro(171,b) = land
    forage(171,b) = land
    u_comp(171,b) = 0.
    v_comp(171,b) = 0.
  ENDDO
!print*,"Made a channel between Australia & Papua New Guinea"
!pause
!check for coherence across variables - fill some gaps in cphyll data.
DO iloop = 1,180
   DO jloop = 1,1080
```

```fortran
                IF ((sst(iloop,jloop).GT.0).AND.(chloro(iloop,jloop).LT.0)) THEN
                   !We have SST but no cphyll...
                   !spatial interpolation of chlorophyll into missing area
                                                                             cphyll(1) =
chloro(iloop-1,jloop-1)
                                                                             cphyll(2) =
chloro(iloop-1,jloop)
                   IF (jloop+1.LE.1080) cphyll(3) = chloro(iloop-1,jloop+1)
                   IF (iloop+1.LE.180)  cphyll(4) = chloro(iloop+1,jloop-1)
                   IF (iloop+1.LE.180)  cphyll(5) = chloro(iloop+1,jloop)
                   IF ((iloop+1.LE.180).AND.(jloop+1.LE.1080)) THEN cphyll(6)=chloro(iloop+1,jloop+1)
                   ENDIF
             cphyll(7) = chloro(iloop,jloop-1)
             IF (jloop+1.LE.1080) cphyll(8) = chloro(iloop,jloop+1)
             !pause
             DO kloop = 1,8
               IF (cphyll(kloop).GE.0.) THEN
                 sum_c  = sum_c + cphyll(kloop)
                 count1 = count1+1
               END IF
             END DO
         IF      (count1.GT.0) THEN
                   !assign mean value of neighbours to missing value
                   chloro(iloop,jloop) = sum_c/count1*1.
         ELSE
                   !There are no neighbouring cphyll values;
                   !check for neighbouring SST values...
                 temp(1) = sst(iloop-1,jloop-1)
                 temp(2) = sst(iloop-1,jloop)
             IF (jloop+1.LE.1080) temp(3) = sst(iloop-1,jloop+1)
             IF (iloop+1.LE.180)  temp(4) = sst(iloop+1,jloop-1)
             IF (iloop+1.LE.180)  temp(5) = sst(iloop+1,jloop)
             IF ((iloop+1.LE.180).AND.(jloop+1.LE.1080)) temp(6)=sst(iloop+1,jloop+1)
             temp(7) = sst(iloop,jloop-1)
             IF (jloop+1.LE.1080)   temp(8) = sst(iloop,jloop+1)
         DO kloop = 1,8
           IF (temp(kloop).GT.0.) THEN
             sum_t  = sum_t + temp(kloop)
             count2 = count2+1
           END IF
         END DO

                     IF (count2.EQ.0) THEN
                       !There are none - flag this square as land
```

```
                       !WRITE(26,*)iloop,jloop,sst(iloop,jloop),chloro(iloop,jloop)
                          !print*,"No neighbouring SST data for:",iloop,jloop
                          !print*,"Setting all variables to:",land
                          sst(iloop,jloop)   = land
                          chloro(iloop,jloop) = land
                          forage(iloop,jloop)     = land
                          u_comp(iloop,jloop) = 0.
                          v_comp(iloop,jloop) = 0.
                          !pause
                       ELSE
!There are SST values around - we are in the sea - keep previous month's cphyll
                          IF (jloop-90.GT.0) THEN
                             chloro(iloop,jloop) = chloro(iloop,jloop-90)
                          ELSE
                             chloro(iloop,jloop) = chloro(iloop,jloop+990)
                          ENDIF
                       !print*,"Temporal interpolation for:",iloop,jloop
                       !pause
                       END IF

                    END IF

                    sum_c       = 0.
                    sum_t       = 0.
                    count1      = 0
                    count2      = 0
                    temp(:)     = 0.
                    cphyll(:)   = -9.

                 ENDIF

              ENDDO
           ENDDO

! Write output data

        WRITE(20,100)    sst(:,:)
        WRITE(21,101)    forage(:,:)
        WRITE(22,100)    chloro(:,:)
        WRITE(23,100)    u_comp(:,:)
        WRITE(24,100)    v_comp(:,:)


! Get data ready for export to animation files (increase scale & flag land as -1)
        sst(:,:)      = sst(:,:)
```

```fortran
      sst(:,:)      = max(-1.,sst(:,:))
      forage(:,:) = 10*forage(:,:)
      forage(:,:) = max(-1.,forage(:,:))
      chloro(:,:) = 10*(chloro(:,:))
      chloro(:,:) = max(-1.,chloro(:,:))
      u_comp(:,:) = 1E2*u_comp(:,:)
   v_comp(:,:) = 1E2*v_comp(:,:)

! Write data for input to RV ANIMATOR

      DO iloop = 1,12
          b = 1+iloop*90-90
          DO jloop = b,b+89
             WRITE(30,102)    (sst(kloop,jloop),kloop = 1,180)
             WRITE(31,102)    (forage(kloop,jloop),kloop = 1,180)
             WRITE(32,102)    (chloro(kloop,jloop),kloop = 1,180)
             WRITE(33,102)    (u_comp(kloop,jloop),kloop = 1,180)
             WRITE(34,102)    (v_comp(kloop,jloop),kloop = 1,180)
          END DO
        WRITE(30,*)
        WRITE(31,*)
        WRITE(32,*)
        WRITE(33,*)
        WRITE(34,*)

      END DO

! -----------------------------------------------------------
      100     FORMAT(180F8.2)
      101     FORMAT(180F10.4)
      102     FORMAT(180F7.1,X)


! -----------------------------------------------------------

      END
```

```fortran
PROGRAM SKIPJACK

IMPLICIT NONE

INTEGER        POP,YEAR,MONTH,DAY,ILOOP,TID
INCLUDE 'comtun.txt'

POP = INITPOP

OPEN (10,file="SKJ.log")
OPEN(1,FILE='OUT/'//'all.txt')
OPEN(2,FILE='OUT/'//'temp.txt')
OPEN(3,FILE='OUT/'//'pop.txt')
OPEN(4,FILE='OUT/'//'attributes.txt')
WRITE(10,*)"Year","Month","Day"

CALL SRAND(123.615)

CALL INITIALISE(POP)

CALL ENVIRONMENT(POP)

!carry on with the program
DO YEAR = 1,HORIZON

  IF(POP==0) EXIT

  DO iloop = 1,POP
    IF (AV(0,ILOOP)==0) print*,"DEAD...:",ILOOP
  END DO
      TID = 0
    DO MONTH = 1,12

      TID = TID + 1

      WRITE(*,*)YEAR,MONTH,POP
      WRITE(3,*)YEAR,MONTH,POP

    DO DAY = 1,MAANE(MONTH)

      !print*,DAY,"POP=",pop
      !print*,1
```

```
        CALL GROWTH  (POP,YEAR,MONTH,DAY)
          !print*,2

          CALL TUNAMOV(POP,YEAR,MONTH,DAY,TID)
            !print*,3

          CALL TUNAREP(POP,YEAR,MONTH,DAY)


          ENDDO
      ENDDO
ENDDO

CLOSE(1)
CLOSE(2)
CLOSE(3)
CLOSE(4)

END PROGRAM SKIPJACK
```

```fortran
!-------------------------------------------

SUBROUTINE INITIALISE(POP)

IMPLICIT NONE

!-------------------------------------------

INTEGER              I,STRING,POP
REAL(8)              RAND,KD
INCLUDE         'comtun.txt'

Kd      = Ky/365.

!Create KROMosomes randomly for initial run....
DO I = 1,POP
  DO STRING = 1,MAXS
    IF(RAND(0).LT.0.5) THEN
      SV(STRING,I) = RAND(0)*2
    ELSE
      SV(STRING,I) = -RAND(0)*2
    ENDIF
  ENDDO
ENDDO

!Provide attributes
DO I = 1,POP
  AV(0,I)   =   1                                    !
  AV(1,I)   =   90+INT(RAND(0)*720)                  !Age in days
      length =  Linf*(1.-exp(-Kd*AV(1,I)))          !length in cm
  AV(2,I)   =   a*length**b                          !Mass in kg - as f(AGE))
  AV(3,I)   =   AV(2,I)*TED*1e3                      !Energy kJ
  AV(8,I)   =   1E6                                  !No. of individuals
  AV(9,I)   =   80.+RAND(0)*40.                      !Position E (0-180)
  AV(10,I) = -20.+RAND(0)*40.                        !Position N (-39-50)
!print*,int(AV(1,I)),AV(2,I),int(AV(3,I)),int(AV(9,I)),int(AV(10,I))
ENDDO

!Provide number of days per month
MAANE(1)  = 31
MAANE(2)  = 28
MAANE(3)  = 31
MAANE(4)  = 30
MAANE(5)  = 31
MAANE(6)  = 30
MAANE(7)  = 31
MAANE(8)  = 31
MAANE(9)  = 30
MAANE(10) = 31
MAANE(11) = 30
MAANE(12) = 31
print*,"Population initialised..."
!print*,int(AV(1,9)),AV(2,9),int(AV(3,9)),int(AV(9,9)),int(AV(10,9))
!pause

END SUBROUTINE INITIALISE
```

```fortran
      SUBROUTINE ENVIRONMENT(POP)

      implicit none

!  Declare variables

      INTEGER    mon_loop,lon_loop,lat_loop,i,j,k,lat,POP,IND
      REAL       temp1(180,1080),temp2(180,1080),temp3(180,1080),temp4(180,1080),temp5(180,1080)
      REAL, PARAMETER:: maxF = 1.
      INCLUDE    'comtun.txt'

!  Open input files

      OPEN(20,FILE='IN/'//'sst.dat')
      OPEN(21,FILE='IN/'//'forage.dat')
      OPEN(22,FILE='IN/'//'chloro.dat')
      OPEN(23,FILE='IN/'//'u_comp.dat')
      OPEN(24,FILE='IN/'//'v_comp.dat')

      DO J=1,1080
      READ(20,'(180(F8.2))') (TEMP1(I,J),I = 1,180)
      READ(21,'(180(F10.4))')(TEMP2(I,J),I = 1,180)
        READ(22,'(180(F8.2))') (TEMP3(I,J),I = 1,180)
      READ(23,'(180(F8.2))') (TEMP4(I,J),I = 1,180)
      READ(24,'(180(F8.2))') (TEMP5(I,J),I = 1,180)
      ENDDO

!  Read input parameters
      DO mon_loop = 1,12
          k = 1+mon_loop*90-90
          DO lon_loop = 1,180
        lat = 50
            DO lat_loop = K,K+89
                sst    (lat,lon_loop,mon_loop)= TEMP1(lon_loop,lat_loop)
                forage(lat,lon_loop,mon_loop)= TEMP2(lon_loop,lat_loop)
                chloro(lat,lon_loop,mon_loop)= TEMP3(lon_loop,lat_loop)
                u_comp(lat,lon_loop,mon_loop)= TEMP4(lon_loop,lat_loop)
                v_comp(lat,lon_loop,mon_loop)= TEMP5(lon_loop,lat_loop)
                lat = lat-1
            END DO
      END DO
      END DO
```

```fortran
!Flag incomplete time series as land

        DO mon_loop = 1,12
           k = 1+mon_loop*90-90
           DO lon_loop = 1,180
         lat = 50
             DO lat_loop = K,K+89
                 IF     (sst(lat,lon_loop,mon_loop)==land) THEN
                   sst    (lat,lon_loop,:)= land
                   forage(lat,lon_loop,:)= land
                   chloro(lat,lon_loop,:)= land
                   u_comp(lat,lon_loop,:)= 0.
                   v_comp(lat,lon_loop,:)= 0.
                 ELSE IF      (chloro (lat,lon_loop,mon_loop)==land) THEN
                   sst    (lat,lon_loop,:)= land
                   forage(lat,lon_loop,:)= land
                   chloro(lat,lon_loop,:)= land
                   u_comp(lat,lon_loop,:)= 0.
                   v_comp(lat,lon_loop,:)= 0.
                 END IF
                 lat = lat-1
             END DO
        END DO
        END DO

        !Create daily increments
        DO mon_loop = 1,11
            DO lon_loop = 1,180
                DO lat_loop = 50,-39,-1
                dsst(lat_loop,lon_loop,mon_loop)     = (1./MAANE(mon_loop))*(sst
(lat_loop,lon_loop,mon_loop+1)-sst    (lat_loop,lon_loop,mon_loop))
                    dforage(lat_loop,lon_loop,mon_loop) =
(1./MAANE(mon_loop))*(forage(lat_loop,lon_loop,mon_loop+1)-forage(lat_loop,lon_loop,mon_loop))
                    dchloro(lat_loop,lon_loop,mon_loop) =
(1./MAANE(mon_loop))*(chloro(lat_loop,lon_loop,mon_loop+1)-chloro(lat_loop,lon_loop,mon_loop))
                    du_comp(lat_loop,lon_loop,mon_loop) =
(1./MAANE(mon_loop))*(u_comp(lat_loop,lon_loop,mon_loop+1)-u_comp(lat_loop,lon_loop,mon_loop))

                    dv_comp(lat_loop,lon_loop,mon_loop) =
(1./MAANE(mon_loop))*(v_comp(lat_loop,lon_loop,mon_loop+1)-v_comp(lat_loop,lon_loop,mon_loop))

                END DO
        END DO
        END DO
```

```fortran
          END DO
          DO lon_loop = 1,180
            DO lat_loop = 50,-39,-1
              dsst    (lat_loop,lon_loop,12) = (1./MAANE(12))*(sst(lat_loop,lon_loop,1)    - sst
(lat_loop,lon_loop,12))
              dforage(lat_loop,lon_loop,12) = (1./MAANE(12))*(forage(lat_loop,lon_loop,1) -
forage(lat_loop,lon_loop,12))
              dchloro(lat_loop,lon_loop,12) = (1./MAANE(12))*(chloro(lat_loop,lon_loop,1) -
chloro(lat_loop,lon_loop,12))
              du_comp(lat_loop,lon_loop,12) = (1./MAANE(12))*(u_comp(lat_loop,lon_loop,1) -
u_comp(lat_loop,lon_loop,12))
              dv_comp(lat_loop,lon_loop,12) = (1./MAANE(12))*(v_comp(lat_loop,lon_loop,1) -
v_comp(lat_loop,lon_loop,12))
            END DO
          END DO

          !check not initialised on land
1         DO IND = 1,POP
            IF (SST(INT(AV(10,IND)),INT(AV(9,IND)),1)==LAND) THEN
              print*,"Starting on land",IND,AV(9,IND),AV(10,IND)
                AV(9,IND)  =  80.
                AV(10,IND) = -20.
              print*,"Position reset",AV(9,IND),AV(10,IND)
              pause
                GOTO 1
            END IF
          END DO

          !Get maximum values for later on.
          maxSST = MAXVAL(SST)
          maxCHL = MAXVAL(chloro)
          maxFI  = MAXVAL(forage)
          maxU   = MAXVAL(ABS(u_comp))
          maxV   = MAXVAL(ABS(v_comp))
          !PRINT*,MAXU,MAXV

100       FORMAT(180F8.2)
101       FORMAT(180F10.4)
102          FORMAT(2X,5F6.3)


END   SUBROUTINE
```

```fortran
!Program to calculate larval mortality, juvenile/adult bioenergetics, and growth.

SUBROUTINE GROWTH(POP,YEAR,MONTH,DAY)

implicit none

INTEGER seed,meal,POP,YEAR,MONTH,DAY,IND,N,E
REAL*4      MPred,MStarv,MTherm,MSen,MFish,dT,TA,TAC,TAF,Nprey,TD
REAL*4   PI,v_range,h,K490,Kd,EncRate,pS,pF,pE,EF
REAL*4      EM,ELn,ELd,SDA,Mmeal,TEDi,REM
INCLUDE 'comtun.txt'

IF(YEAR<7) THEN
  TD = 0.5
ELSEIF(YEAR<20) THEN
  TD = 0.7
ELSEIF(YEAR<30) THEN
  TD = 0.9
ELSEIF(YEAR<40) THEN
  TD = 1.
ELSE
  TD = 1.1
ENDIF


!DAILY INSTANTANEOUS MORTALITY RATES
!M1 = 0.6          !days 1    to  7
!M2 = 0.4          !days 8    to  14
!M3 = 0 !.2        !days 15   to  21
!M4 = 0 !.1        !days 22   to  45
!M5 = 0.001        !days 46   to  90
!M6 = 0.0001       !days 91   to  360
!M7 = 0.00001      !days 361 to  1440


PI =   3.14159


!initialise
Kd       = Ky/365.                    !daily instantaneous growth rate
seed = 123456787            !seed for random number generation
pS       = 0.                          !random number

!Start calculations
```

```
DO IND = 1,POP
   IF (AV(0,IND)==1) THEN                !only do calcs for superI that are alive

   AV(1,IND) = AV(1,IND) + 1             !they get one day older

   E = INT(AV(9,IND))
   N = INT(AV(10,IND))

 !Interpolation to daily values (TA,TAC,TAF) from monthly climatologies
   IF(DAY<15) THEN
   IF(MONTH==1) THEN
       TA  = SST(N,E,12)      + 1.*((MAANE(12)-15)+DAY)*DSST(N,E,12)
       TAF = FORAGE(N,E,12) + 1.*((MAANE(12)-15)+DAY)*DFORAGE(N,E,12)
       TAC = CHLORO(N,E,12) + 1.*((MAANE(12)-15)+DAY)*DCHLORO(N,E,12)
       IF (TAC.LT.0) THEN
         print*,"Chlorophyll has gone negative..."
         !print*,ind,day,E,N,AV(1,IND),AV(2,IND),AV(3,IND),AV(8,IND)
         print*,ind,month,day,E,N,AV(1,IND),TAC,TA,TAF
         !print*,CHLORO(N,E,12),CHLORO(N,E,1),CHLORO(N,E,2)
         pause
         !TAC = 2.
       END IF
     ELSEIF(MONTH>1) THEN
       TA  = SST(N,E,MONTH-1)     + 1.*((MAANE(MONTH-1)-15)+DAY)*DSST(N,E,MONTH-1)
       TAF = FORAGE(N,E,MONTH-1) + 1.*((MAANE(MONTH-1)-15)+DAY)*DFORAGE(N,E,MONTH-1)
       TAC = CHLORO(N,E,MONTH-1) + 1.*((MAANE(MONTH-1)-15)+DAY)*DCHLORO(N,E,MONTH-1)
       IF (TAC.LT.0) THEN
         print*,"Chlorophyll has gone negative..."
         !print*,ind,day,E,N,AV(1,IND),AV(2,IND),AV(3,IND),AV(8,IND)
         print*,ind,month,day,E,N,AV(1,IND),TAC,TA,TAF
         !print*,CHLORO(N,E,MONTH-1),CHLORO(N,E,MONTH),CHLORO(N,E,MONTH+1)
         pause
         !TAC = 2.
       END IF
     ENDIF
   ELSE !DAY > 15
       TA  = SST(N,E,MONTH)     + 1.*(DAY-15)*DSST(N,E,MONTH)
       TAF = FORAGE(N,E,MONTH) + 1.*(DAY-15)*DFORAGE(N,E,MONTH)
       TAC = CHLORO(N,E,MONTH) + 1.*(DAY-15)*DCHLORO(N,E,MONTH)
   ENDIF
```

```fortran
IF (TA.LT.20)          THEN
  dT = 20.- TA
ELSEIF (TA.GT.30) THEN
  dT = TA - 30.
END IF

!Age based calculations of growth & mortality
IF(AV(1,IND).LE.90) THEN                              !Stage 1.  Planktonic larvae

   length = Linf*(1.-exp(-Kd*AV(1,IND)))          !Von Bert length

   IF (length==0) THEN
     print*,"Length is zero"
     pause
   END IF

   !Three mechanisms of natural mortality :
   MPred  = TAF/length                                      !predation
   MStarv = 0.025/TAC                                       !starvation
   MTherm = 0.025*EXP(dT)                                   !thermal stress
   IF((TA>20).AND.(TA<30)) MTherm = 0              !within optimal temp. range
   !kill some individuals in this superI
   AV(8,IND)=max(0.,AV(8,IND)*EXP(-(MPred+MStarv+MTherm)*TD))
   !PRINT*,IND,AV(8,IND),AV(1,IND)

ELSE                                 !Stage 2.  Non-buoyant nektonic juveniles/adults

   length = (AV(2,IND)/a)**(1./b)                       !Length-based predation risk

     IF (YEAR>10) THEN
     IF (length.LT.30.) THEN
     MPred  = TAF/length
     AV(8,IND) = max(0.,AV(8,IND)*EXP(-MPred*TD))
     END IF
     END IF

   !BIOENERGETICS

   !1. SMR

   EM = 24.*14.054*412.*(AV(2,IND)**0.563)*1e-3       !E lost in kJ/24 hrs > AV2 in kg
```

```
!2.     LOCOMOTION

!2 * 12 hr periods; speed in BL/s
!E = time * constant * length**1.5 * velocity**2.5

ELn=(12.*c*length**1.5)*(1.*length**2.5)* 1e-3      !kJ/12hrs @ nightime > speed = 1 BL/s
ELd=(12.*c*length**1.5)*(3.*length**2.5).* 1e-3     !kJ/12hrs @ daytime  > speed = 3 BL/s


!3.  FEEDING

!calculate prey concentration
Nprey = MAX(1E-10,TAF*1e-7)                !converts from forage index (0-1) to shoals/m**3

!calculate depth integrated visual range, 1 < r < 30
k490    = 0.022 + 0.119*TAC**1.122                          !Austin & Petzold, 1981
h       = 4.6/k490                                    !h = first attenuation depth

v_range = EXP(-k490*h)-1.
v_range = MIN(30., MAX(1.,SQRT((-10./k490)*v_range)))

!calculate probability of finding food

EncRate = 0.5*(3.*Nprey*PI*v_range**2.)

pF = (1.-EXP(-EncRate*2.16e4))/TD

Mmeal = min(0.3,(0.05*AV(2,IND)))                    !stomach volume = 5% of body weight

DO meal=1,2
   CALL RANDOM_NUMBER(pE)                            !probability of encountering food
      IF (pE.LE.pF) THEN                             !it finds food
         Ef   = 1.*Mmeal*1e3*PED                     !energy gain (kJ) through feeding
         SDA     = 0.2*EM                            !energy loss (kJ) by SDA
         AV(3,IND) =  AV(3,IND) + Ef - SDA           !net gain/loss in energy density
                                                     !FOR EACH MEAL
      END IF
END DO

!print energy budget
   !print*,"E+:",Ef
```

```
    !print*,"E-:",EM+ELn+ELd
    !pause


    !Update energy after total metabolic losses in this time step
AV(3,IND) = AV(3,IND) - (EM+ELn+ELd)


!Update structural weight
AV(2,IND) = max(AV(2,IND),1e-3*(AV(3,IND)/TED))


!IF (AV(2,IND).GT.45) THEN
  !print*,DAY,IND
    !PRINT*,IND,"is getting too fat, weighing",AV(2,IND),"kg."
!  pause
!ELSE IF (AV(2,IND).LT.1) THEN
!PRINT*,IND,"is getting too thin, weighing",AV(2,IND),"kg."
  !pause
!ENDIF


!Death by starvation - MStarv as exponential function of energy density
  TEDi    = AV(3,IND)/(1e3*AV(2,IND))
  TEDi    = MAX(0.,(TEDi - 3.))
  MStarv   = EXP(-1.5350567*TEDi)
  AV(8,IND) = MAX(0.,AV(8,IND)*EXP(-MStarv*TD))


!Death by thermal stress
MTherm = 0.025*EXP(dT)                              !thermal stress
  IF((TA>20).AND.(TA<30)) MTherm = 0               !within optimal temp. range
AV(8,IND)=max(0.,AV(8,IND)*EXP(-MTherm*TD))        !kill some individuals in this superI


  !Implement spatially uniform, length-based fishing mortality
  MFish = 0.
  IF ((length.GT.20.).AND.(length.LE.30.)) THEN
    MFish =  1./365.
  ELSE IF ((length.GT.30.).AND.(length.LE.40.)) THEN
    MFish =  2./365.
  ELSE IF (length.GT.40.) THEN
    MFish =  1./365.
  END IF
  AV(8,IND) = MAX(0.,AV(8,IND)*EXP(-MFish*TD))
```

```fortran
      !implement age-dependent mortality i.e. senescence forcing function
      IF (AV(1,IND).GT.1080) THEN
        MSen       = 15./365.
        AV(8,IND) =      MAX(0.,AV(8,IND)*EXP(-MSen*TD))
      END IF

   END IF            !different age groups (LARVAE OR JUVENILES/ADULTS)

   rem = MOD(YEAR,2)
   IF ((REM==0.).AND.(MONTH==1).AND.(DAY==1)) THEN
        print*,"Age (days) of ind.",ind,int(AV(1,IND))
        !PAUSE
   ENDIF

   !kill superI if no more individuals
   IF(AV(8,IND)<10) AV(0,IND) = 0

  END IF            !if alive
 END DO             !Do IND = 1,POP

END   SUBROUTINE GROWTH
```

```fortran
!-------------------------------------------------------------------

SUBROUTINE TUNAMOV(POP,YEAR,MONTH,DAY,TID)

implicit none

!-------------------------------------------------------------------

INTEGER      POP,E,N,YEAR,I,MONTH,HID,IN,OUT,DAY,S,TID,DE,DN,MATE
REAL         TA,TAC,TAF,NYE,NYN,MASS,DIST
REAL         U00,U10,U01,U11,V00,V10,V01,V11,YFAK,XFAK,UADV,VADV
INCLUDE      'comtun.txt'

  !Calculate planktivore mortality and food intake
  DO 81 I = 1,POP
     IF(AV(0,I)==0) GOTO 81

     !Set new habitats
     N = INT(AV(10,I))
   E = INT(AV(9,I))

     !Interpolation to daily values from monthly climatologies
     IF(DAY<15) THEN
    IF(MONTH==1) THEN
        TA  = SST(N,E,12)                      + (MAANE(12)-15+DAY)*DSST(N,E,12)
        TAC = CHLORO(N,E,12)         + (MAANE(12)-15+DAY)*DCHLORO(N,E,12)
        TAF = FORAGE(N,E,12)         + (MAANE(12)-15+DAY)*DFORAGE(N,E,12)

        U00 = U_COMP(N,E,12)         + (MAANE(12)-15+DAY)*DU_COMP(N,E,12)
        U10 = U_COMP(N,E+1,12)       + (MAANE(12)-15+DAY)*DU_COMP(N,E+1,12)
        U01 = U_COMP(N+1,E,12)       + (MAANE(12)-15+DAY)*DU_COMP(N+1,E,12)
        U11 = U_COMP(N+1,E+1,12)     + (MAANE(12)-15+DAY)*DU_COMP(N+1,E+1,12)
        V00 = V_COMP(N,E,12)         + (MAANE(12)-15+DAY)*DV_COMP(N,E,12)
        V10 = V_COMP(N,E+1,12)       + (MAANE(12)-15+DAY)*DV_COMP(N,E+1,12)
        V01 = V_COMP(N+1,E,12)       + (MAANE(12)-15+DAY)*DV_COMP(N+1,E,12)
        V11 = V_COMP(N+1,E+1,12)     + (MAANE(12)-15+DAY)*DV_COMP(N+1,E+1,12)
     ELSEIF(MONTH>1) THEN
        TA  = SST(N,E,MONTH-1)         + (MAANE(MONTH-1)-15+DAY)*DSST(N,E,MONTH-1)
        TAC = CHLORO(N,E,MONTH-1)      + (MAANE(MONTH-1)-15+DAY)*DCHLORO(N,E,MONTH-1)
        TAF = FORAGE(N,E,MONTH-1)      + (MAANE(MONTH-1)-15+DAY)*DFORAGE(N,E,MONTH-1)

        U00 = U_COMP(N,E,MONTH-1)        + (MAANE(MONTH-1)-15+DAY)*DU_COMP(N,E,MONTH-1)
        U10 = U_COMP(N,E+1,MONTH-1)   + (MAANE(MONTH-1)-15+DAY)*DU_COMP(N,E+1,MONTH-1)
```

```fortran
       U01 = U_COMP(N+1,E,MONTH-1)   + (MAANE(MONTH-1)-15+DAY)*DU_COMP(N+1,E,MONTH-1)
       U11 = U_COMP(N+1,E+1,MONTH-1) + (MAANE(MONTH-1)-15+DAY)*DU_COMP(N+1,E+1,MONTH-1)
       V00 = V_COMP(N,E,MONTH-1)        + (MAANE(MONTH-1)-15+DAY)*DV_COMP(N,E,MONTH-1)
       V10 = V_COMP(N,E+1,MONTH-1)   + (MAANE(MONTH-1)-15+DAY)*DV_COMP(N,E+1,MONTH-1)
       V01 = V_COMP(N+1,E,MONTH-1)   + (MAANE(MONTH-1)-15+DAY)*DV_COMP(N+1,E,MONTH-1)
       V11 = V_COMP(N+1,E+1,MONTH-1) + (MAANE(MONTH-1)-15+DAY)*DV_COMP(N+1,E+1,MONTH-1)
     ENDIF
    ELSE
       TA  = SST(N,E,MONTH)               + (DAY-15)*DSST(N,E,MONTH)
       TAC = CHLORO(N,E,MONTH)          + (DAY-15)*DCHLORO(N,E,MONTH)
       TAF = FORAGE(N,E,MONTH)          + (DAY-15)*DFORAGE(N,E,MONTH)

       U00 = U_COMP(N,E,MONTH)           + (MAANE(MONTH)-15+DAY)*DU_COMP(N,E,MONTH)
       U10 = U_COMP(N,E+1,MONTH)         + (MAANE(MONTH)-15+DAY)*DU_COMP(N,E+1,MONTH)
       U01 = U_COMP(N+1,E,MONTH)         + (MAANE(MONTH)-15+DAY)*DU_COMP(N+1,E,MONTH)
       U11 = U_COMP(N+1,E+1,MONTH)   + (MAANE(MONTH)-15+DAY)*DU_COMP(N+1,E+1,MONTH)
       V00 = V_COMP(N,E,MONTH)           + (MAANE(MONTH)-15+DAY)*DV_COMP(N,E,MONTH)
       V10 = V_COMP(N,E+1,MONTH)         + (MAANE(MONTH)-15+DAY)*DV_COMP(N,E+1,MONTH)
       V01 = V_COMP(N+1,E,MONTH)         + (MAANE(MONTH)-15+DAY)*DV_COMP(N+1,E,MONTH)
       V11 = V_COMP(N+1,E+1,MONTH)   + (MAANE(MONTH)-15+DAY)*DV_COMP(N+1,E+1,MONTH)
     ENDIF
     DN = 0
DE = 0

    !Values for spatial interpolation (Hansen & Aadlandsvik 1996)

    !Bilinear interpolation
    XFAK = AV(9,I)  - NINT(AV(9,I)) + 0.5
YFAK = AV(10,I) - NINT(AV(10,I)) + 0.5
    UADV = U00 + XFAK*(U10-U00) + YFAK*(U01-U00) + XFAK*YFAK*(U00-U10-U01+U11)
VADV = V00 + XFAK*(V10-V00) + YFAK*(V01-V00) + XFAK*YFAK*(V00-V10-V01+V11)
    !PRINT*,E,N,MONTH,U_COMP(N,E,MONTH)

    !Convert advective distance to km, then to degrees
    UADV = 1e-3*UADV*86400/111.*cos(AV(10,I))  !divide by lengthscale
VADV = 1e-3*VADV*86400/111.                          !divide by lengthscale
!Segregate larvae and adults
IF(AV(1,I)<90) THEN                                  !Drifting larvae

    !Larval movement determined solely by advection
    NYE = AV(9,I)+UADV
NYN = AV(10,I)+VADV
```

```
        ELSE                                              !Will powered juveniles and adults

        !Input variables standardised by maximum values
        INPUT(1) = TA/maxSST*1.                                       !TEMPERATURE
        INPUT(2) = E/IMAX*1.                                          !POSITION
        INPUT(3) = N/JMAX*1.                                          !-- " --
        INPUT(4) = (AV(3,I)/AV(2,I))/TED                      !CONDITION
        INPUT(5) = TAF/MAXFI                          !CONDITION
        INPUT(6) = (TID-183)/183.

          !k490   = 0.022 + 0.119*TAC**1.122                  !VISUAL RANGE
            !h        = 4.6/k490
            !v_range = EXP(-k490*h)-1.
            !v_range = MIN(30., MAX(1.,SQRT( (-10./k490)*v_range) ) )
            !INPUT(5) = v_range/30.

        !INPUT(3) = TAF/maxFI
        !INPUT(4) = AV(2,I)/6.

        S = 1
        DO HID = 1,NUMHID                                     !Hidden nodes
            SUMVEKT(HID) = 0
            DO IN = 1,NUMIN                                        !Input nodes
             SUMVEKT(HID) = SUMVEKT(HID)+INPUT(IN)*SV(S,I)
             S = S + 1
            ENDDO
            IF(SUMVEKT(HID).LT.-50) SUMVEKT(HID) = -50
          SUMVEKT(HID) = (1./(1.+EXP(-(SUMVEKT(HID)+SV(S,I)))))
            S = S + 1
        ENDDO

        DO OUT = 1,NUMOUT                                     !Output nodes
          OUTPUT(OUT) = 0.
          DO HID = 1,NUMHID
           OUTPUT(OUT) = OUTPUT(OUT) + SUMVEKT(HID)*SV(S,I)
             S = S + 1
            ENDDO
        ENDDO

        DN = NINT(ATAN(OUTPUT(1))*0.94)                              !north-south
movement
        DE = NINT(ATAN(OUTPUT(2))*0.94)                              !east-west
movement
```

```
!MATE = NINT((1./(1.+EXP(-(OUTPUT(3))))))

!Calculate length        (cm)
MASS   = AV(2,I)                              !kg
LENGTH = (mass/a)**(1/b)             !cm

!Calculate distance moved @ mean speed = 2 BL/s
DIST   = 1e-5*(LENGTH*2*86400.)

!Calculate new position
IF((DN==1).AND.(DE==0)) THEN
 NYN = AV(10,I) + DIST/111. + VADV
 NYE = AV(9,I) + UADV
ELSEIF((DN==1).AND.(DE==1)) THEN
 NYN = AV(10,I) + SIN(45.)*DIST/111.+ VADV
 NYE = AV(9,I)+ SIN(45.)*DIST/111*COS(AV(10,I)) + VADV        + UADV
ELSEIF((DN==1).AND.(DE==-1)) THEN
 NYN = AV(10,I) + SIN(45.)*DIST/111.
 NYE = AV(9,I) - SIN(45.)*DIST/111*COS(AV(10,I))
ELSEIF((DN==0).AND.(DE==0)) THEN
 NYN = AV(10,I) + VADV
 NYE = AV(9,I)
ELSEIF((DN==0).AND.(DE==1)) THEN
 NYN = AV(10,I) + VADV
 NYE = AV(9,I) + DIST/111*COS(AV(10,I))
ELSEIF((DN==0).AND.(DE==-1)) THEN
 NYN = AV(10,I) + VADV
 NYE = AV(9,I) - SIN(45.)*DIST/111*COS(AV(10,I))
ELSEIF((DN==-1).AND.(DE==0)) THEN
 NYN = AV(10,I) - DIST/111. + VADV
 NYE = AV(9,I)
ELSEIF((DN==-1).AND.(DE==1)) THEN
 NYN = AV(10,I) - SIN(45.)*DIST/111.
 NYE = AV(9,I)+ SIN(45.)*DIST/111*COS(AV(10,I)) + VADV
ELSEIF((DN==-1).AND.(DE==-1)) THEN
 NYN = AV(10,I) - SIN(45.)*DIST/111.
 NYE = AV(9,I) - SIN(45.)*DIST/111*COS(AV(10,I)) + VADV
ENDIF

ENDIF        !Stage loop

!PRINT*,1,AV(9,I),AV(10,I)
!Do not allow movement onto land
```

```fortran
      IF((NYN.GT.50).OR.(NYN.LT.-39)) THEN                      !At boundary of domain
       AV(10,I)  = AV(10,I)
       AV(9,I)  = AV(9,I)
      ELSEIF((NYE.GT.180).OR.(NYE.LT.1)) THEN                   !At boundary of domain
       AV(10,I)  = AV(10,I)
       AV(9,I)  = AV(9,I)
      ELSEIF(SST(INT(NYN),INT(NYE),MONTH)==LAND) THEN           !On land
       AV(10,I)  = AV(10,I)
       AV(9,I)  = AV(9,I)
      ELSE
       AV(10,I)  = NYN                                                       !N
       AV(9,I)  = NYE                                                   !E
      ENDIF
       !PRINT*,2,DE,DN,AV(9,I),AV(10,I)
      !IF (SST(int(AV(10,I)),int(AV(9,I)),month)==land) THEN
      !print*,i,"is on land at:",int(AV(10,I)),int(AV(9,I))
      !pause
      !ENDIF


   81 CONTINUE

      !Write output data for individuals and environment
      IF(YEAR==HORIZON) THEN
         WRITE(1,*)
         WRITE(2,*)
         !Write individual characteristics to file
         IF(DAY==15) THEN
          DO I = 1,POP
           WRITE(4,'(10(F11.2,X))')AV(:,I)
          ENDDO
         ENDIF

         DO N = 50,-39,-1
           DO E = 1,180
             SUML(E) = 0.
             !SUMZ(E) = 0.
               DO I = 1,POP
                IF((INT(AV(9,I))==E).AND.(INT(AV(10,I))==N)) SUML(E) = SUML(E)+2
             ENDDO
               !IF(DAY<15) THEN
             ! IF(MONTH==1) THEN
               !  SUMZ(E)  = SST(N,E,12)   + (MAANE(12)-15+DAY)*DSST(N,E,12)
               ! ELSEIF(MONTH>1) THEN
```

```
            !   SUMZ(E)   = SST(N,E,MONTH-1) + (MAANE(MONTH-1)-15+DAY)*DSST(N,E,MONTH-1)
            ! ENDIF
            !ELSE
            ! SUMZ(E)   = SST(N,E,MONTH) + (DAY-15)*DSST(N,E,MONTH)
            !ENDIF
        IF(SST(N,E,MONTH)==LAND) SUML(E) = -1.
        IF(SUML(E)==0.)                    SUML(E) = 1
        !IF(SUMZ(E)==LAND) SUMZ(E) = -1.
        !SUMZ(E)  = SUMZ(E)*0.3
          ENDDO
      WRITE(1,'(180(F7.1,X))')(SUML(E),E = 1,180)
      !WRITE(2,'(180(F7.1,X))')(SUMZ(E),E = 1,180)
    ENDDO
  ENDIF

END SUBROUTINE TUNAMOV
```

```fortran
!-------------------------------------------------------------------

SUBROUTINE TUNAREP(POP,YEAR,MONTH,DAY)

IMPLICIT NONE

!-------------------------------------------------------------------


INCLUDE        'comtun.txt'
INTEGER        POP,YEAR,MONTH,DAY,IND,I,L,M,ILOOP
INTEGER        PARTNER,NEWPOP,FI(MPOP),BREAK,STRING
INTEGER        COMP,NYPOP,R
REAL           RAND,BATCH

NEWPOP = 0
DO IND = 1, POP
  IF(AV(0,IND)==1) THEN

     !IF ((YEAR==10).AND.(MONTH==1).AND.(DAY==1)) THEN
     !PRINT*,"In TUNAREP loop"
     !print*,"POP:",pop
     !endif

     !Reproduce if the time and size is ok
     PARTNER = 0
     length = (AV(2,IND)/a)**(1./b)

     IF(length.GE.SAM) THEN
       DO L = 1,POP
         PARTNER = INT(POP*RAND(0)+1)
       ENDDO
     ENDIF

     !Calculate batch fecundity
     BATCH = 0
     IF(PARTNER.GT.0) THEN
       BATCH = INT(AV(2,IND)*RBF)               !no. of individuals in this batch
         IF(BATCH>1e6) BATCH = 1e6
         AV(3,IND) = AV(3,IND)*0.98             !Spawning penalty

     !Carry out chromosomal variation for new individuals
     I = NEWPOP+POP+1
```

```
      IF(I.GT.MPOP) GOTO 1

      !Cross over SVsomes between partners
      IF(RAND(0).LT.RECOM) THEN
        BREAK = INT(RAND(0)*MAXS)+1        !Initialise random break piece at SVsomes
        IF(RAND(0)<0.5) THEN
          DO STRING = 1,MAXS
            IF(STRING.LE.BREAK) THEN
                SV(STRING,I) = SV(STRING,IND)
              ELSE
              SV(STRING,I) = SV(STRING,PARTNER)
              ENDIF
          ENDDO
        ELSE
            DO STRING = 1,MAXS
            IF(STRING.LE.BREAK) THEN
                SV(STRING,I) = SV(STRING,PARTNER)
              ELSE
              SV(STRING,I) = SV(STRING,IND)
              ENDIF
          ENDDO
        ENDIF
      ELSE
        DO STRING = 1,MAXS
          SV(STRING,I) = SV(STRING,IND)
        ENDDO
      ENDIF

      !Perform random mutations
      DO M = 1,MAXS
        IF(RAND(0).LE.MUTE) THEN
            IF(RAND(0)<0.5) THEN
          SV(M,I) = SV(M,I)+RAND(0)
            ELSE
          SV(M,I) = SV(M,I)-RAND(0)
            ENDIF
        ENDIF
      ENDDO

      !Initialise new individuals with attribute vectors
      AV(0,I) = 1                                              !All in new population
are alive
      AV(1,I) = 1                                              !        .
```