

On the Integrated Study of Tuna Behaviour and Spatial Dynamics: Tagging and Modelling as Complementary Tools

David S. Kirby^{1,2,3}

¹*Fisheries Research Group, Department of Biology, University of Leicester, UK.*

²*Earth Observation Science Group, Department of Physics, University of Leicester, UK.*

³*National Institute of Water and Atmospheric Research (NIWA) Ltd., Wellington, NZ*

Correspondence: < d.kirby@SCIENCEnet.com >

Key words: tuna, behaviour, tagging, modelling

Abstract: In this paper, modelling efforts that seek to describe, explain and predict the behaviour and spatial dynamics of tunas are reviewed and discussed in relation to tagging 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 we simply will not be able to derive and validate 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 we must assess reproductive motivation, 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 and enable us to understand these fish. This synthesis will only be achieved through collaboration between scientists with individual skills in field, laboratory and computational ecology and with innovative technical support. Some case studies are presented here to support this thesis, and it is hoped that this paper will stimulate discussion, collaboration and the development of new observational and computational methodologies.

1. INTRODUCTION

It has long been a goal of tuna ecologists to fully describe the behaviour of these magnificent fish 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.*, 1986). 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 and 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 one 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 and 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 Figure 1. Theoretical models in behavioural ecology (*e.g.* Kirby *et al.*, 2000) 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 and Marsac, 1993).

In this paper I discuss differences in modelling methodologies and emphasise the common ground that can exist between observational and computational studies. 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.

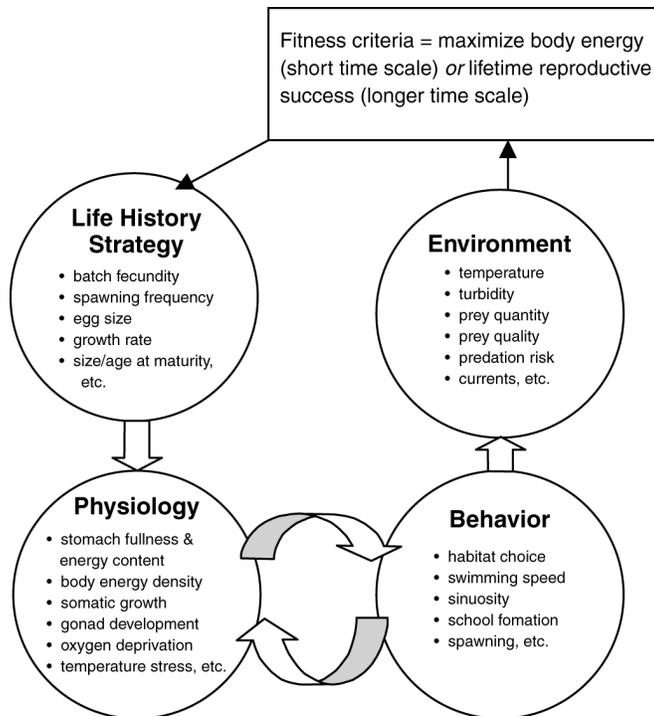


Figure 1. Conceptual model for the behavioural ecology of tunas. The properties of the oceanic environment interact with physiological constraints and evolutionary imperatives. In order to maximise some measure of fitness, a predatory fish comes to optimise its use of available habitat, through natural selection against sub-optimal strategies, and by making cognitive choices within the constraints of its sensory and learning abilities.

2. OBSERVATIONS OF TUNAS IN THE OCEAN AND IN THE LABORATORY

There is a long history of observations of tunas at sea and in the laboratory, and the ongoing development of dedicated facilities, research programs and databases will ensure that as long as we keep our minds open, we will continue to further our knowledge and understanding. This is not a comprehensive review of observational studies, but instead I have highlighted key studies that are central to my thesis *viz.* that the right variables must be

measured at sea, in order to be able to derive and evaluate models that represent a true understanding of tuna behaviour and spatial dynamics.

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 and 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, 1994; 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 and 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 two 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) 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 one 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 (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 one yellowfin and two 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 and Barnard, 1987) — being sexually immature, these fish certainly aren't 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 animal is observed.

3. MODELS FOR THE BEHAVIOUR AND SPATIAL DYNAMICS OF TUNAS

Model: a simplified description of a system, process, *etc.*, put forward as a basis for theoretical or empirical understanding; a conceptual or mental representation of something. (Math.) A set of entities that satisfies all the formulae of a given formal or axiomatic system. (Oxford English Dictionary, 1993)

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 and clarify the relative importance of different parameters and processes about which we previously had only a conceptual understanding. Simpler models often provide insight that is more valuable than accurate numerical fits, and the most influential models are often the ones where the numerical output is not needed to guide the qualitative understanding (Hilborn and Mangel, 1997).

Herein lies the truth that there are many different types of model that may be applied to any particular question. Most scientists will be familiar with the exercise of trying to find correlations between variables, and are happy when measurements of one variable can be used to reduce the variance in measurements of another (some use the term ‘explain’ — I prefer not to). But it is extremely difficult to find statistical relationships that hold in highly variable environments (Sharp, 1995; Mangel *et al.*, 2000; see Bigelow *et al.*, 1999; Andrade and Garcia, 1999). Furthermore, while statistical relationships may describe relationships well or badly, they cannot be used to show causality (Sharp, 1995; Brill, 1997; Hilborn and Mangel, 1997). The researcher 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; Figure 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. There is a body of literature on this subject that is well worth reviewing before undertaking any kind of modelling exercise (*e.g.* citations above, plus Loehle, 1983 and reviews by Tyler and Rose, 1994, Giske *et al.*, 1998, Mangel *et al.*, 2000; Huse *et al.*, in press).

Models for the behaviour and spatial dynamics of tunas are many and varied (Deriso *et al.*, 1991; Cayré and Marsac, 1993; Dagorn *et al.*, 1995, 1997; Bertignac *et al.*, 1998; Dagorn and Freon, 1999; Sibert *et al.*, 1999; Stöcker, 1999; Humston *et al.*, 2000; Kirby *et al.*, 2000). Rule-based methods have been used to investigate both fine-scale behaviour of tunas (Dagorn *et al.*, 1995; Dagorn and 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 skipjack tuna (*Katsuwonus pelamis*) builds on earlier levels of modelling, covering general circulation (Blanke and 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 and 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 a recent theoretical modelling exercise (Kirby *et al.*, 2000), 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), sensory systems (visual range), and both biotic and abiotic characteristics of the environment (prey abundance and energy density, water temperature and turbidity) were included. We 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 and Clark, 1988; Clark

and Mangel, 2000; Kirby *et al.*, 2000). The exercise was started 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, we succeeded in predicting behaviour from physiology in a complex environment, and inadvertently developed the optimal foraging model envisaged by Hunter *et al.* (1986; p. 30). The model itself 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; and the optical and nutritional properties of forage), but it is the first model for tunas that predicts behaviour from physiology and environment; it is this kind of model that 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 and 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.

4. MEANS TOWARDS A TRUE UNDERSTANDING OF TUNAS: A NEW SYNTHESIS

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 and 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 paper, 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 mentioned above, in an optimal foraging model for tunas at fronts (Kirby *et al.*, 2000) we needed 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. In addition, the model makes predictions, in particular regarding state-dependent behaviour, for which comparable observations are not presently available. We therefore hope that in future sea-going work, researchers will adopt the model, or at least the approach, and use it to guide their investigations.

Joseph and 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 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 biogeographical areas, we should have progressed our techniques by now 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 sinuosity. 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 and Wild, 1984). Different models may be used to investigate these different aspects of movement. An optimal foraging model (*e.g.* Kirby *et al.*, 2000) 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, if the fitness-based modelling approach is still followed, a Darwinian fitness measure must be adopted (*e.g.* number of eggs laid per gram body mass above size at maturity—Fiksen *et al.*, 1995; Figure 1) and either an optimisation or an adaptation approach used (Giske *et al.*, 1998).

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.

ACKNOWLEDGEMENTS

I would like to acknowledge all those whose work is referred to in this paper and I hope that this discussion will be a constructive stimulus towards further research. I am grateful to the reviewers for their comments and to John Sibert for encouraging me to commit my thoughts to paper.

REFERENCES

- Andrade, H.A., and Garcia, C.A.E. (1999) Skipjack tuna fishery in relation to sea surface temperature off the southern Brazilian coast. *Fish. Oceanogr.* **8**(4), 245–254.
- Atema, J., Holland, K. and Ikehara, W. (1980) Olfactory responses of Yellowfin tuna (*Thunnus albacares*) to prey odors: chemical search image. *J. Chem. Ecol.* **6**(2), 457–465.
- Barkley, R.A., Neill, W.H., and Gooding, R.M. (1978) Skipjack tuna, *Katsuwonus pelamis*, habitat based on temperature and oxygen requirements. *Fish. Bull.* **76**(3), 653–662.
- Bertignac, M., Lehodey, P., and Hampton, J. (1998) A spatial population dynamics model of tropical tunas using a habitat index based on environmental parameters. *Fish. Oceanogr.* **7**(3–4), 326–334.
- Bigelow, K.A., Boggs, C.H., and He, X. (1999) Environmental effects on swordfish and blue shark catch rates in the US North Pacific longline fishery. *Fish. Oceanogr.* **8**(3), 178–198.
- Blackburn, M. (1965) Oceanography and the ecology of tunas. *Oceanogr. Mar. Biol. Ann. Rev.* **3**, 299–322.
- Blanke, B., and Delecluse P. (1993) variability of the tropical Atlantic Ocean simulated by a general circulation model with two different mixed-layer physics. *J. Phys. Oceanogr.* **23**, 1363–1388.
- Block, B.A., Keen, J.E., Castillo, B., Dewar, H., Freund, E.V., Marcinek, D.J., Brill, R.W. and Farwell, C. (1997) Environmental preferences of yellowfin tuna (*Thunnus albacares*) at the northern extent of its range. *Mar. Biol.* **130**, 119–132.
- Block, B.A., Dewar, H., Freund, Farwell, C. and Princes, E.D. (1998a) A new satellite technology for tracking the movements of Atlantic bluefin tuna. *Proc. Natl Acad. Sci. USA*, **95**, 9384–9389.
- Block, B.A., Dewar, H., Williams, T., Princes, E.D. Farwell, C. and Fudge, D. (1998b) Archival Tagging of Atlantic Bluefin Tuna (*Thunnus thynnus thynnus*). *Mar. Technol. Soc. J.*, **32**(1), 37–46.
- Brill, R.W. (1987) On the standard metabolic rate of tropical tunas, including the effect of body size and acute temperature change. *Fish. Bull.* **85**, 25–35.
- Brill, R.W. (1997) How tuna physiology affects tuna movements and distribution. Pelagic Fisheries Research Program, University of Hawaii, Newsletter **2**, 4.
- Brill, R.W. (1994) A review of temperature and oxygen tolerance studies of tunas pertinent to fisheries oceanography, movement models and stock assessments. *Fish. Oceanogr.* **3**(3), 204–216.
- Brill, R.W., Lowe, T.E. and Cousins, K.L. (1998) *How water temperature really limits the vertical movements of tunas and billfishes - it's the heart stupid!* American Fisheries Society, International Congress on Biology of Fish, Towson University, Baltimore, MD. Abstract available: http://www.soest.hawaii.edu/PFRP/brill_afs.pdf
- Brill, R.W., Block, B.A., Boggs, C.H., Bigelow, K.A., Freund, E.V. and Marcinek, D.J. (1999) Horizontal movements and depth distribution of large adult yellowfin tuna (*Thun-*

- nus albacares*) near the Hawaiian Islands recorded using ultrasonic telemetry: implications for the physiological ecology of pelagic fishes. *Mar. Biol.* **133**, 395–408
- Carey, F.G. and Lawson, K.D. (1973) Temperature regulation in free swimming bluefin tuna. *Comp. Biochem. Physiol.* **44**, 375–392.
- Cayré, P. and Marsac, F. (1993) Modelling the yellowfin tuna (*Thunnus albacares*) vertical distribution using sonic tagging results and local environmental parameters. *Aquatic Living Resources* **6**, 1–14.
- Clark, C.W. and Mangel, M. (2000) *Dynamic State Variable Models in Ecology*. Oxford University Press Inc., USA, 302 pp.
- Dagorn, L., Petit, M., Stretta, J-M., Bernadet, X. and Romos, A.G. (1995) Toward a synthetic eco-ethology of tropical tunas. *Sci. Mar.*, **59**(3–4), 335–346.
- Dagorn, L., Petit, M., Stretta, J-M. (1997) Simulation of large-scale tropical tuna movements in relation with daily remote sensing data: the artificial life approach. *Biosystems*, **44**, 167–180.
- Dagorn, L., and Fréon, P. (1999) Tropical tuna associated with floating objects: a simulation study of the meeting point hypothesis. *Can. J. Fish. Aquat. Sci.*, **56**, 984–993.
- Dagorn, L., Bach, P., and Josse, E. (2000) Movement patterns of large bigeye tuna (*Thunnus obesus*) in the open ocean, determined using ultrasonic telemetry. *Mar. Biol.* **136**, 361–371.
- Deriso, R.B., Punsly, R.G., and Bayliff, W.H. (1991) A Markov movement model of Yellowfin tuna in the Eastern Pacific Ocean and some analyses for international management. *Fish. Res.*, **11**, 375–395.
- Dewar, H., Graham, J.B., and Brill, R.W. (1994) Studies of tropical tuna swimming performance in a large water tunnel. *J. Exp. Biol.* **192**, 33–44.
- Dizon, A.E., Neill, W.H., and Magnuson, J.J. (1977) Rapid temperature compensation of volitional swimming speeds and lethal temperatures in tropical tunas (Scombridae). *Env. Biol. Fishes* **2**, 83–92.
- Fielder, P., and Bernard, H. (1987) Tuna aggregation and feeding near fronts observed in satellite imagery. *Cont. Shelf Res.* **7**, 871–881.
- Fiksen, Ø., Giske, J., and Slagstad, D. (1995) A spatially explicit fitness-based model of capelin migrations in the Barents Sea. *Fish. Oceanogr.* **4**(3), 193–208.
- Giske, J., Huse, G., and Fiksen, Ø. (1998) Modelling spatial dynamics of fish. *Rev. Fish Biol. Fisher.*, **8**, 57–91.
- Hampton, J. (2000) Natural mortality rates in tropical tunas: size really does matter. *Can. J. Fish. Aquat. Sci.*, **57**, 1002–1010
- Hilborn, R., and M. Mangel (1997) *The Ecological Detective: Confronting Models with Data*. Princeton University Press, USA, 315 pp.
- Holland, K.N., Brill, R.W., and Chang, R.K.C. (1990) Horizontal and vertical movements of Yellowfin and Bigeye tuna associated with fish aggregating devices. *Fish. Bull.* **88**, 493–507.
- Holland, K.N., Brill, R.W., Chang, R.K.C., Sibert, J.R., and Fournier, D.A. (1992) Physiological and behavioural thermoregulation in bigeye tuna (*Thunnus obesus*). *Nature* **358**, 410–411.
- Humston, R., Ault, J.S., Lutcavage, M., and Olson, D.B. (2000) Schooling and migration of large pelagic fishes relative to environmental cues. *Fish. Oceanogr.*, **9**(2), 136–146.
- Hunter, J.R., Argue, A.W., Bayliff, W.H., Dizon, A.E., Fonteneau, A., Goodman, D., and Seckel, G.R. (1986) The dynamics of tuna movements: an evaluation of past and future research. *FAO Fisheries Technical Paper* **277**, 78 pp.
- Huse G., and Giske, J. (1998) Ecology in Mare Pentium: An individual-based spatio-temporal model for fish with adapted behaviour. *Fish. Res.* **37**(1–3), 163–178.
- Huse, G., Giske, J., and Salvanes, A.G.V. (in press) Individual-based modelling. In Hart, P.J.B., and J.D. Reynolds (eds.), *Fish and Fisheries Handbook*, Blackwell Science, UK.

- Joseph, J., and Wild, A. (1984) Considerations for Tuna Research to the Year 2000. Inter-American Tropical Tuna Commission. La Jolla, CA.
- Josse, E., Bach, P., and Dagorn, L. (1998) Simultaneous observations of tuna movements and their prey by sonic tracking and acoustic surveys. *Hydrobiologia*, **371/372**, 61–69.
- Kirby, D.S., Fiksen, Ø., and Hart, P.J.B. (2000) A dynamic optimisation model for the behaviour of tunas at ocean fronts. *Fish. Oceanogr.* **9**, 4., 328–342.
- Kishinouye, E. (1923) Contributions to the comparative study of the so-called scombroid fishes. *J. Coll. Agric. Imp. Univ. Tokyo*. **8**, 293–475.
- Krebs, J.R., Davies, N.B., and Parr, J. (1993) *Introduction to Behavioural Ecology*. Blackwell Science, UK, 432 pp.
- Krebs, J.R., and Davies, N.B. (1997) *Behavioural Ecology*. Blackwell Science, UK, 464 pp.
- Lauris, R.M., Fielder, P.C., and Montgomery, D.R. (1984) Albacore tuna catch distributions relative to environmental features observed from satellites. *Deep-Sea Res.* **31**(9), 1085–1099.
- Lehodey, P., Andre, J.-M., Bertignac, M., Hampton, J., Stoens, A., Menkes, C., Memery, L., and Grima, N. (1998) Predicting skipjack tuna forage distributions in the equatorial Pacific using a coupled dynamical bio-geochemical model. *Fish. Oceanogr.* **7**(3/4), 317–325.
- Loehle, C. (1983) Evaluation of theories and calculation tools in ecology. *Ecol. Model.*, **19**, 239–247.
- Lowe (2000) Blood oxygen-binding characteristics of Bigeye tuna (*Thunnus obesus*), a high-energy-demand teleost that is tolerant of low ambient oxygen. *Mar. Biol.* **136**, 1087–1098.
- Lutcavage, M. (1997) Distribution, relative abundance, and behavior of giant bluefin tuna in New England waters, 1995. Coll. Vol XLVI, **2**, 332–347. *Int. Comm. Conserv. Atlantic Tunas*, Madrid.
- Mangel, M., and Clark, C.W. (1988) *Dynamic Modeling in Behavioural Ecology*. Monographs in Behaviour and Ecology, Princeton University Press, Princeton, New Jersey, 308 pp.
- Mangel, M., Fiksen, Ø., and Giske, J. (2000) Logical, statistical and theoretical models in natural resource management and research. In Franklin, A., and Schenk, T. (Eds.), *How to Practice Safe Modelling*. Island Press, Boulder, CO.
- Magnuson, J.J. (1973) Comparative study of adaptations for continuous swimming and hydrostatic equilibrium of scombroid and xiphoid fishes. *Fish. Bull.* **71**, 337–356.
- Marchal, E., Gerlotto, F. and Stequert, B. (1993) On the relationship between scattering layer, thermal structure and tuna abundance in the Eastern Atlantic equatorial current system. *Oceanol. Acta*, **16**(3), 261–272.
- SERG (2000) URL: <http://www.ifm.uib.no/Staff/giske/SERG2000.htm>
- Sharp, G.D. (1995) It's about time: new beginnings and old good ideas in fisheries science. *Fish. Oceanogr.* **4**(4), 324–341.
- Sibert, J.R., Hampton, J., Fournier, D.A., and Bills, P.J. (1999) An advection-diffusion-reaction model for the estimation of fish movement parameters from tagging data, with application to skipjack tuna (*Katsuwonus pelamis*). *Can. J. Fish. Aquat. Sci.*, **56**, 6, 925–938.
- Stöcker, S. (1999) Models for tuna school formation. *Math. Biosci.* **156**, 167–190.
- Stoens A., Menkes C., Dandonneau, Y., and Memery, L. (1998) New production in the equatorial Pacific: a coupled dynamical-biogeochemical model. *Fish. Oceanogr.* **7**(3/4) 311–316.
- Sund, P.N., Blackburn, M., and Williams, F. (1981) Tunas and their environment in the Pacific Ocean: a review. *Oceanogr. Mar. Biol. Ann. Rev.* **19**, 443–512.
- Tyler, J.A., and Rose, K.A. (1994) Individual variability and spatial heterogeneity in fish population models. *Rev. Fish Biol. Fisher.*, **4**, 91–123.