REVIEWS

Towards more efficient longline fisheries: fish feeding behaviour, bait characteristics and development of alternative baits

Svein Løkkeborg · Sten Ivar Siikavuopio ·
Odd-Børre Humborstad · Anne
Christine Utne-Palm · Keno Ferter

Abstract Better knowledge of food search behaviour in fish is essential for studies that aim to improve longline fishing, particularly through bait development. This review provides an overview of our understanding of how fish detect and locate sources of food odour, focusing on the stimuli and sensory modalities involved, and on factors that affect feeding activity. Studies that identify feeding attractants and efforts to develop alternative longline baits are presented. The review reveals that such studies are few in number, and that to date there are no alternatives to traditional baits in commercial long-lining despite the growing demand for these resources, which are also used for human consumption. The chemical compounds that elicit food search behaviour differ from species to species, and species selectivity could be improved by incorporating specific feeding attractants in manufactured baits. The unique properties of chemical stimuli and odour dispersal form the basis for improving longline efficiency through the development of a long-lasting bait. Vision is important in prey capture, and manufactured baits can be made more visible than natural baits by increasing the contrast (e.g. via fluorescent or polarising coatings) and creating motion through buoyancy. Physical properties such as size, shape, texture and strength can also be manipulated in a manufactured bait to improve catch efficiency. Knowledge obtained from studies of various aspects of food search behaviour is of paramount importance for future research aimed at alternative bait development and improving longline fishing.

Introduction

The bait is the key factor in longline fishing as this fishing method is highly dependent on the feeding behaviour of the target species. However, common bait types such as squid, mackerel and herring are also used for human consumption. There is growing demand for these food sources, and bait prices have greatly increased in the course of the past decade. There is therefore a great need for alternative longline baits that are not based on resources used for human consumption. Ideally, an alternative bait should be effective, species- and size-selective, practical for storage and baiting, and based on low-cost surplus

S. Løkkeborg (✉) · O.-B. Humborstad ·
A. C. Utne-Palm · K. Ferter
Institute of Marine Research, P.O. Box 1870,
5817 Bergen, Norway
e-mail: svein.lokkeborg@imr.no

S. I. Siikavuopio
Nofima Marin, P.O. Box 6122, 9291 Tromsø, Norway

K. Ferter
Department of Biology, University of Bergen,
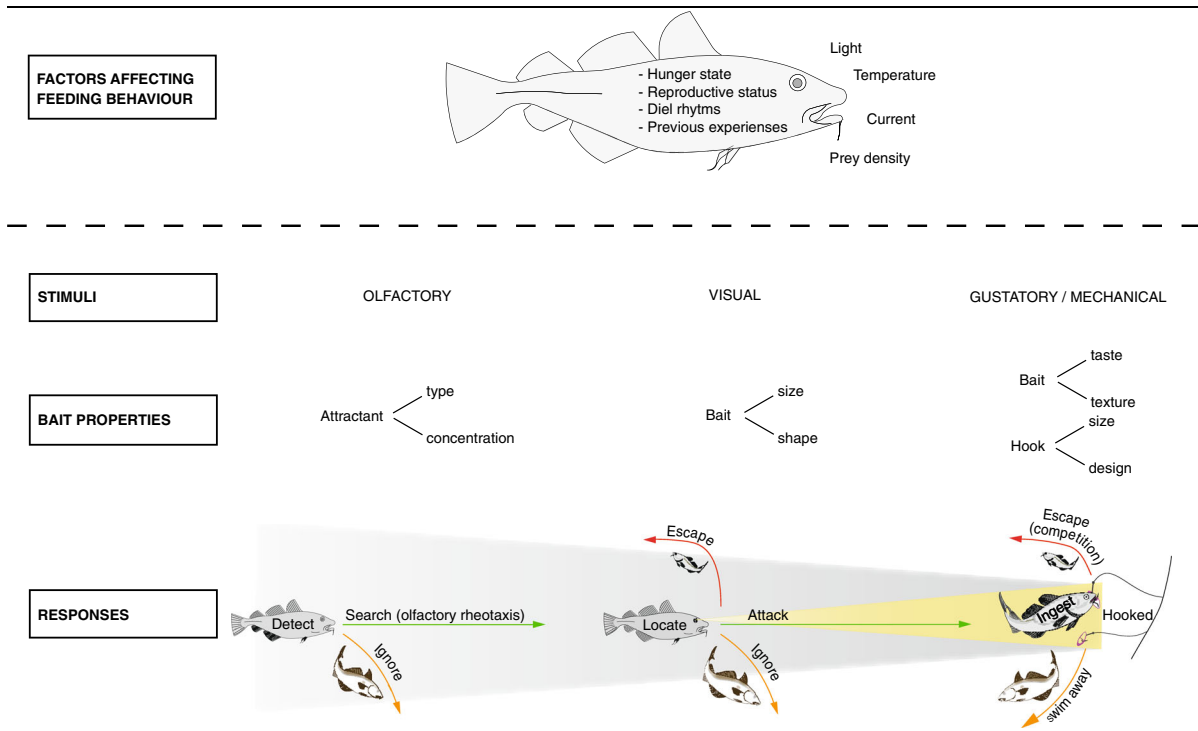P.O. Box 7803, 5020 Bergen, Norway

Fig. 1 Fish behaviour to baited hooks—a multitude of interacting variables. Variables (internal and external) that affect fish behavior are shown above the *broken line*. Stimuli, bait properties and responses are shown at different distances down-current of the baited hooks. *Grey* and *yellow shades* illustrate odour plume and visual range, respectively. Redrawn from Løkkeborg et al. (2010)

products. A bait meeting these criteria would make longline fishing more environmentally friendly.

Several efforts have been made to develop a longline bait based on surplus products or artificial attractants (e.g. Løkkeborg 1990a, 1991; Januma et al. 2003; Erickson and Berkeley 2008; Henriksen 2009), but to date no alternative to traditional baits for use in commercial longline fisheries has emerged. The development of alternative baits to replace traditional baits is challenging, as the capture efficiency of longline baits depends on several factors. An alternative bait needs to be based on an odour source that releases feeding attractants that elicit food search behaviour in the target species. In addition, it must release these attractants over a considerable period of time (i.e. several hours) which is often achieved by using a binder (see Løkkeborg 1990b). Taste, texture and size are also important factors that encourage fish to approach and swallow baited hooks. Finally, the bait must have sufficient physical resilience to withstand foraging by seabirds and benthic scavengers.

As longline fishing depends on the demand for food in the target species, knowledge of food search behaviour in fish is the basis of bait development efforts. Here we review current understanding of how fish detect, approach and locate a food odour source, focusing on the stimuli and sensory modalities involved (chemoreception, vision, mechanoreception) and on factors affecting feeding activity (see Fig. 1). We also review how fish respond to bait characteristics such as size, shape and texture, and include insights derived from recreational angling.

Finally, we discuss studies that identify the chemical nature of feeding attractants in fish and efforts to develop alternative baits for longline fisheries. Although descriptions of these studies are scarce, our review focuses on work of particular interest to bait development efforts, with the aim of providing a useful background for future initiatives to develop new bait types. Such knowledge is also of importance for efforts to improve longline fishing in general.

The basis for longline fishing: chemoreception, chemical stimuli and food search

Chemoreception

The olfactory and gustatory systems comprise the major chemosensory pathways in fish (Hara 1994). Their detailed morphologies differ considerably among species, reflecting adaptations to a wide range of environments and evolutionary pathways. Thus, the gross morphology and functions given here for the olfactory and gustatory systems should be accompanied by rereading the reviews of e.g. Hara (1992, 1994, 2011) and Hino et al. (2009).

Olfaction is facilitated by two paired nostril structures in the snout of the fish, each of which has an anterior inlet and a posterior outlet. Various mechanisms (forward movements, currents, respiratory pressure changes) cause water to flow through these channels, and waterborne chemicals are detected by the specialised bipolar neurone receptor cells of the nasal mucosa (Zeiske et al. 1992). Signals from these receptor cells are transferred directly via the cranial nerve I to the olfactory bulb of the brain, where the information is processed (Hara 1992).

Taste buds form the structural basis of the gustatory system. They can be found on the lips, in the oral cavity, the pharynx, on the barbels, fins, gills and sometimes, as in scaleless catfish, all over the body surface. Chemical information detected by these specialized epithelial cells is transmitted to the central nervous system by the cranial nerves VII (facial), IX (glossopharyngeal), and X (vagal).

As both olfactory and gustatory senses are mediated by waterborne low-molecular compounds (sometimes the same ones), it can be difficult to identify the specific role played by each of the senses in the propagation of a specific behaviour. Although care should be taken with generalisations, some features of each of the systems seem to be consistent over a wide range of species. Based on its lower detection thresholds (Johnstone 1980; Ishida and Kobayashi 1992), olfaction is believed to initiate food search behaviour for a wide variety of odours, while the gustatory system seems to be more selective and provides the final sensory evaluation (i.e. odours may trigger food search, however the gustatory system may reject the object after tasting it) (Kasumyan and Døving 2003).

Chemical stimuli

Chemical stimuli and chemoreception are of particular importance for the detection and location of small, stationary food items such as baits. Fishing with bait (i.e. longlines and pots) is common in deep waters, during the polar winter and in habitats of high turbidity, all of which are conditions with limited visibility.

A chemical stimulus, as opposed to visual and acoustic stimuli, has two properties that are crucial for the use of bait to capture fish. First, a chemical stimulus disperses over long ranges and can be detected by fish from very long distances. For example, longlines baited with mackerel have been shown to attract cod (*Gadus morhua*) from a distance of 700 m (Løkkeborg 1998). Another behavioural study indicated that sablefish (*Anoplopoma fimbria*) were capable of responding to odours from squid baits at a distance of several hundred metres (Løkkeborg et al. 1995). In contrast, both visual and acoustic (except low-frequency sounds) stimuli attenuate rapidly. Second, a chemical stimulus lasts for a long period of time, whereas visual and acoustic signals fade immediately after being transmitted. Cod that responded to baits from a distance of 700 m located the baits 7 h after the longline was set, showing that bait odours last for many hours (Løkkeborg 1998). These two properties are unique to chemical stimuli, and form the basis of longlining as a stationary fishing method that has long spatial and temporal ranges. In the development of new and more efficient alternative baits it is important to take these distinctive features of longline fishing into account.

Olfactory food-search behaviour and odour source location

The fact that fish are able to detect and respond to baits from a long distance means that they must have a functional mechanism which enables them to locate odour sources. Unlike visual and acoustic signals, chemical stimuli have no directional cues associated with its chemical signature. The particle motion component of underwater sounds is a vector quantity that provides the basis for directional hearing in fish (Hawkins 1986), whereas odours carry no directional information per se. Thus, upon entering a bait odour source, the fish depends on additional cues and employs several sensory modalities.

The current is the main agent for dispersion of chemicals in seawater because the rate of diffusion in water is very low. Thus, aquatic organisms that are activated by chemical stimuli need to move upstream to locate the stimulus source (Atema 1980). Rheotaxis is a behavioural orientation to water currents, and chemically stimulated rheotaxis is regarded as the most likely mechanism used by fish and crustaceans to locate odour sources (Carton and Montgomery 2003; Løkkeborg et al. 2010). There is evidence that rheotaxis in fish is mediated by the lateral line system (Montgomery et al. 1997), and studies have demonstrated the use of both olfactory and mechanosensory systems in olfactory search behaviour (Baker and Montgomery 1999; Baker et al. 2002). Field observations of several species have demonstrated that fishes often approach an odour source downstream of the release point (Fernö et al. 1986; Løkkeborg et al. 1989; Løkkeborg and Fernö 1999). Behavioural field studies that used acoustic transmitters to monitor the movements of cod showed that cod that encountered a bait odour plume downstream located the bait twice as often as cod that were upstream and out of range of the plume, indicating the importance of chemically mediated food searching (Løkkeborg 1998).

Gradient search, where the animal reacts to a concentration gradient that increases as the distance to the odour source decreases, has been suggested as an alternative mechanism to locate odour sources. However, this explanation is less likely because turbulence often renders gradients weak and inconsistent, and thus creates a highly intermittent and complex chemical signal (Webster and Weissburg 2001; Carton and Montgomery 2003).

The mechanisms that fish use to locate baited gear have important practical consequences for longline gear operations, e.g. how baited longlines are set in relation to the current direction and tidal cycle. Therefore, efforts to develop alternative baits should also take these aspects of food search behaviour into account.

Visual food-search behaviour

In spite of the general poor quality of underwater images, most fish species depend on vision as one source of sensory information (Guthrie and Muntz 1993). Detection of a prey item requires the predator to detect a difference in contrast between the prey and its background. Because seawater absorbs long and short wavelengths more than intermediate wavelengths (i.e. <430 and >530 nm) (Jerlov 1968), light becomes monochromatic at moderate depths (Lythgoe 1975). Thus, brightness and contrast tend to be the determining factors of visibility under water (Hemmings 1965; Lythgoe 1975).

Visual detection depends on several factors such as the fish's visual capacity, the physical/optical characteristics of the environment (light intensity, wavelength composition and turbidity) and prey characteristics (size, movement, contrast and colour). Behavioural studies have shown that the distance from which an animal responds to an object increases with increasing light intensity (Vinyard and O'Brien 1976; Confer et al. 1978), but at a progressively decreasing rate as light saturation is reached (i.e. a log–linear relationship) (Utne 1997). Particles in the water (i.e. turbidity) absorb and scatter light, and the visual range decreases with increasing turbidity in a log–linear relationship (Vinyard and O'Brien 1976; Gregory and Northcote 1993; Utne 1997).

Coastal waters contain relatively long wavelengths (appearing green to yellow) due to high levels of decaying organic matter, silt and suspended particles, which absorb shorter wavelengths, while oceanic waters (low in particles) transmit mainly shorter wavelengths therefore appearing blue (Jerlov 1968). A fish will see much more sharply (better contrast) if it is more sensitive to that part of the spectrum that water absorbs least. Thus, the spectral sensitivity of the visual pigments in fish is related to their habitat, the depth at which they live and the visual tasks of the species (Lythgoe 1984). Coastal species have visual pigments with peak absorption in the green part of the spectrum, while the pigments of oceanic and deepwater fish have peak absorption in the blue (Denton and Warren 1956; Munz and McFarland 1977). Studies have shown that a small shift in the peak wavelength of the available light can have significant effects on prey detection (Utne-Palm and Bowmaker 2006).

Fish use rod vision (grey-scale vision) at night and cone vision (colour vision) during daylight hours. Thus, to improve interest in and detection of a prey or bait, we need to consider (1) when the species is most active (a nocturnal, diurnal or crepuscular hunter), and (2) on the basis of its peak in activity, which colour will offer the best contrast to the background

lightning. Fish probably evolved colour vision to enhance contrast (McFarland and Munz 1975), and the prey colour therefore affects the maximum reaction distance (Utne-Palm 1999). Knowledge of the visual pigments of the target species (i.e. the spectral sensitivity) and the spectral range of its prey and its environment are thus of great importance. For best visual detection, we should therefore choose a bait/ lure colour that matches the dominant wavelength of the fishing depth.

Theoretically, a greater maximum detection distance should be expected for larger prey, as larger prey will stimulate more of the retina (Lazzaro 1987), and experimental studies have shown that prey size has a positive effect on reaction distance (Vinyard and O'Brien 1976; Utne 1997). The visual capacity of fish has also been shown to be size-dependent, as visual range is found to increase as fish grow (Hairston et al. 1982; Breck and Gitter 1983). A larger eye has better acuity because both the lens and retinal cone density increase with size (Hairston et al. 1982). Furthermore, the lens of a larger eye is located further from the retina, which increases image size (Easter et al. 1977).

Many marine species, including crustaceans, cephalopods and fish, can detect and respond to polarised light (Cronin and Shashar 2001; Kamermans and Hawryshyn 2011; see also Shashar et al. 2011). Polarisation can be beneficial in three general areas that are relevant to behavioural manipulation of fish in relation to prey capture: (1) contrast enhancement, (2) visual communication (social interaction), and (3) spatial orientation and navigation (Kamermans and Hawryshyn 2011). Shashar et al. (2000) showed that polarisation of light reflected from fish scales helps cuttlefish to detect their prey, and suggested that polarisation vision is used to break the counter-shading camouflage of light-reflecting silvery fish. Juvenile rainbow trout (*Oncorhynchus mykiss*) also use polarised light to enhance detection of planktonic prey (copepods) (Flamerique and Browman 2001).

UV light (360–400 nm) may also have a positive effect on visual detection. When ultraviolet light shines on a fluorescent substance, the substance absorbs the light and re-emits it, in most cases, at a longer wavelength, which makes it visible to targets that cannot see UV light. Although it is rapidly attenuated in water, sufficient intensity remains in clear water to sustain vision at depths of 100 m and beyond (Losey et al. 1999).

Movement is another factor that is known to have a positive effect on prey detection. Many studies have shown that prey activity or movement increases prey detection distance (Wright and O'Brien 1982; Howick and O'Brien 1983; Holmes and Gibson 1986; Crowl 1989: Utne-Palm 1999). Prey movement has also been found to have a positive effect on a predator's willingness to attack (O'Brian et al. 1976; Rimmer and Power 1978; Scott 1987). In a goby species (*Gobiusculus flavescens*) prey movement was the determining factor for whether or not an attack was induced after prey detection (Utne-Palm 2000). A field study on hooking behaviour showed that haddock (*Melanogrammus aeglefinus*) which were hooked and struggled to escape were subsequently attacked by larger cod (Løkkeborg et al. 1989). This type of attack is not only triggered by increased visual stimulation, but also by greater motivation to attack a struggling or wounded prey.

Mechanoreception and food-search behaviour

All fishes have a mechanosensory lateral line system which is specialised for the detection of water disturbances. Due to the viscosity and density of water, disturbances created by the presence of potential prey and other moving objects are detected via mechanoreception. However, the operational range of the lateral line system is usually restricted to one or at most two body lengths from the object (Kalmijn 1988). The importance of lateral-line-mediated behaviour is likely to increase in deep waters and habitats of high turbidity.

The capability and importance of the lateral line system are most obvious in behaviours related to predator/prey interactions and orientation (Montgomery et al. 1995). Stationary objects such as baits do not create disturbances that resemble those of moving prey items. However, Montgomery et al. (1995) demonstrated an advantage of predatory fish facing upstream as immobile prey sitting on the bottom could still be located, presumably by the downstream perturbations they created. This observation indicates that the lateral line system may assist food-searching fish in locating a stationary bait odour source.

The lateral line system is also believed to play an important role in orientation. Fish that maintain visual or tactile contact with the substrate could in principle use the lateral line to determine current direction and

Table 1 Summary of the factors affecting feeding behaviour and the respective references

Factor	Species	Type of study	Stimuli/key words	References
Feeding motivation and hunger state	Pike (*Esox lucius*)	Laboratory	Prey size	Hart and Connellan (1984)
	Halibut (*Hippoglossus stenolepis*)	Laboratory	Dead squid/light intensity	Stoner (2003)
	Sablefish (*Acnoplopoma fimbria*)	Laboratory	Olfactory/ swimming activity	Løkkeborg et al. (1995)
	Red hake (*Urophysis chuss*)	Laboratory	Olfactory/clam extract	Pearson et al. (1980)
	Australian Salmon (*Arripis trutta*)	Laboratory	Size of krill swarms	Morgan and Ritz (1984)
	Stickleback (*Gasterostesu aculeatus*)	Laboratory	Prey swarm size and predator	Heller and Milinski (1979)
	Atlantic cod (*Gadus morhua*)	Field	Baited long line	Engås and Løkkeborg (1994)
	Atlantic cod (*Gadus morhua*)	Field	Longline fisheries	Steingrund et al. (2009)
	Tunas (*T. alalunga*, *T. obesus*, *T. albacores*)	Field	Longline fisheries	Bertrand et al. (2002)
Temperature	Sablefish (*Acnoplopoma fimbria*)	Laboratory	Olfactory	Stoner and Sturm (2004)
	Atlantic cod (*Gadus morhua*)	Laboratory	Dead capelin/ search activity	Castonguay and Cyr (1998)
	Grass carp (*Ctenopharynodon idella*)	Laboratory	Plant food/ preference	Adamek et al. (1990)
	Atlantic salmon (*Salmo salar*)	Laboratory	Diel light rhythms	Fraser et al. (1993)
Diel, tidal and annual rhythms	Atlantic salmon (*Salmo salar*)	Laboratory	Temperature	Fraser et al. (1993)
	Whiting (*Gadus merlangus*)	Field	Baited hooks/ spawning season	Fernö et al. (1986)
	Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*)	Field	Baited hooks/ spawning season	Løkkeborg et al. (1989)
	Arctic char (*Salvelinus alpines*)	Laboratory	Seasonal/diel feeding activity	Jørgensen and Jobling (1989)
	Atlantic cod (*Gadus morhua*)	Field	Diel changes/ acoustic tags	Løkkeborg and Fernö (1999)
	Pike (Esox lucius)	Field	Angling/moon phase	Kuparinen et al. (2010)
	Killifish (*Fundulus heteroclitus*)	Field	Current	Wiseberg et al. (1981)
Light level	Halibut (*Hippoglossus stenolepis*)	Laboratory	Dead squid	Stoner (2003)
	Largemouth bass (*Micropterus salmoides*)	Laboratory	Time and depth	McMahon and Holanov (1995)
	Walleye pollock (*Theragra chalcogramma*) and sablefish (*Acnoplopoma fimbria*)	Laboratory	Artemia/nocturnal feeding	Ryer and Olla (1999)
Seasonal change in photoperiod	Atlantic salmon (*Salmo salar*)	Laboratory	Photoperiod/ growth	Villarreal et al. (1988)

Table 1 continued

Factor	Species	Type of study	Stimuli/key words	References
	Arctic char (*Salvelinus alpines*)	Laboratory	Photoperiod/ growth	Sæther et al. (1996)
	Perch (*Perca fluviatilis*)	Laboratory	Photoperiod/ growth	Karas (1990)
	Atlantic salmon (*Salmo salar*)	Laboratory	Photoperiod/ growth hormones	Komourdjian et al. (1976)
	Atlantic cod (*Gadus morhua*)	Field	Season/activity	Løkkeborg et al. (1989)
	Arctic char (*Salvelinus alpinus*)	Field	Seasonal growth	Jørgensen et al. (1997)
Water currents	Whiting (*Gadus merlangus*)	Field	Current/baited hooks	Fernö et al. (1986)
	Haddock (*Melanogrammus aeglefinus*)	Field	Current/vertical distribution	Michalsen et al. (1996)
	Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*)	Field	Current strength/ baited hooks	Løkkeborg et al. (1989)
	Killifish (*Fundulus heteroclitus*)	Field	Tidal	Wiseberg et al. (1981)

strength (Montgomery et al. 1995). Baker and Montgomery (1999) demonstrated that the superficial lateral line system controls rheotaxis insofar as pharmacological blockade of the neuromast receptors reduced the rheotactic response. Mechanoreception thus plays an important role both in upstream odour search and in the final location of odour source.

Factors affecting feeding behaviour (summarized in Table 1)

Feeding motivation

Fish do not feed continuously, but in distinct bouts or meals (Jobling et al. 2010). Food deprivation has been shown to affect food searching behaviour and responsiveness to prey in several fish species (Atema 1980; Pearson et al. 1980; Hart and Connellan 1984; Hart 1986). Sablefish responded to lower bait odour concentrations when tested after 4 days of food deprivation, compared to when fed to satiation (Løkkeborg et al. 1995). Also response intensity (swimming speed and turning rate) and the duration of the response to bait odour increased in sablefish with increasing food deprivation (Løkkeborg et al.

1995; Stoner and Sturm 2004). These effects of hunger state affect the distance from which fish start a food search, the search pattern itself, location time and time spent searching for the odour source. Thus, as hunger increases, fish intensify their search behaviour.

Longline fishermen have experienced extremely low catches of cod in the Barents Sea in early spring when the cod are preying on dense schools of capelin (Engås and Løkkeborg 1994), and fishermen from the Faeroe Islands have observed lower catch rates in years of high prey density (Steingrund et al. 2009). Similarly, longline tuna catch rates were low in areas of the tropical Pacific where prey densities were high (Bertrand et al. 2002).

Changes in feeding motivation occur over a wide range of time-scales, from minute-to-minute adjustments made during the course of ingesting a meal to the large changes in food intake that are associated with life history events, e.g. maturation (Jobling et al., 2010). Changes in feeding motivation can also be rhythmically adapted to daily, tidal or annual cycles (Jobling 1994; Houlihan et al. 2001; Jobling et al. 2010). Food intake and the strength of response to baits have been shown to be low during the spawning period, which may reflect seasonal variations in feeding motivation (Fernö et al. 1986; Løkkeborg et al. 1989).

Temperature

Within a normal range of physiological tolerance, temperature can have significant effects on activity, swimming speed, feeding and other fundamental behaviours relevant to baited fishing gears (Stoner 2004; Løkkeborg et al. 2010). The swimming activities of most fish species increase with rising temperature (within limits) (Castonguay and Cyr 1998; Stoner 2004). Food intake normally also increases with temperature, leading to stronger responses to baited gear and a higher probability of being caught (Brett 1979; Stoner 2004; Løkkeborg et al. 2010). Temperature can also have an effect on taste preferences in fish. For example, grass carp (*Ctenopharyngodon idella*) displayed different preferences for the same food items in warm and cold water (Adamek et al. 1990). Furthermore, temperature can affect feeding periodicity in fishes (Fraser et al. 1993). The catchability of baited gears may therefore be strongly affected by temperature through a variety of mechanisms (Stoner 2004).

Diel rhythm, light level and seasonal feeding patterns

Cod and several other species exhibit a diel rhythm in swimming and feeding activity (Eriksson 1978; Thorpe 1978; Jørgensen and Jobling 1989; Løkkeborg et al. 1989; Løkkeborg and Fernö 1999). In autumn the swimming speed of adult cod, which was assumed to reflect food search behaviour, increased at dawn, remained high during the day, then gradually decreased during the evening, and remained low throughout the night (Løkkeborg and Fernö 1999). A fishing experiment performed in a commercial fishery showed that longlines set before dawn caught twice as much haddock as those set later in the day (Løkkeborg and Pina 1997). Changes in food intake according to the phases of moon have also been reported, with food intake peaking a few days before the new and full moon (Leatherland et al. 1992; Kuparinen et al. 2010).

Light level, mediated by vision and contrast, can have direct effects on behaviour patterns like activity, swimming speeds and feeding propensity. Several economically important fish species have low light thresholds for visual feeding (Stoner 2004), but many species have been shown to be relatively unsuccessful in locating and attacking baits in the dark (McMahon

and Holanov 1995; Ryer and Olla 1999; Stoner 2003). The locomotory activity of Pacific halibut (*Hippoglossus stenolepis*), as observed in an experimental laboratory study, was higher at high, rather than low lights levels, and the fish located a larger proportion of the baits offered as the light level increased (Stoner 2003). Thus, light may have a direct effect on longline catchability, and light conditions can lead to differences in catch rates independent of diel rhythms (Stoner 2004).

Seasonal variations in feeding related to changes in the photoperiod have also been demonstrated in several fish species (Villarreal et al. 1988; Karas 1990; Sæther et al. 1996). In general, food intake increases with the lengthening of the photoperiod in spring, and decreases as it shortens in autumn (Komourdjian et al. 1976; Higgins and Talbot 1985). Cod displayed a longer period of high activity during the day in September than in December (Løkkeborg et al. 1989). Seasonal effects on food intake have also been documented in salmonids. For example, anadromous Arctic charr (*Salvelinus alpinus alpinus*) feed intensely and grow rapidly during a short period of their summer residence in the sea and return to fresh water during the winter, when they do not usually feed (Jørgensen et al. 1997).

Water currents

Currents are of great importance to fishing with baits in three ways. First, currents are the most important agent for dispersing olfactory cues in seawater, and a long odour plume can only be created when the current velocity is above a certain minimum. Fernö et al. (1986) reported higher responses to bait in whiting (*Merlangius merlangus*) during periods of current compared to periods of still water. Second, current direction provides an important cue that guides upstream movement towards an odour source. Third, the current can have a direct impact on the food-search strategy in fish due to its effect on swimming activity. As food-searching fish swim predominantly upstream to the odour source, it would be energetically advantageous to be active during periods of moderate or low current velocity, and to remain in shelter when the current is strong. Løkkeborg et al. (1989) showed that when currents were more rapid than 18 cm s^{-1}, the number of cod and haddock attracted to bait was three times less than periods of weaker currents. Tidal

currents can also affect the vertical distribution of cod and haddock (Michalsen et al. 1996). Tidal rhythms in feeding activity are often related to vertical and horizontal movements of prey that use tidal currents to migrate (Gibson 1992). An example of tidally synchronised feeding rhythms is the killifish (*Fundulus* sp.), in which gut content varies in parallel with the tidal cycle (Wiseberg et al. 1981).

Physical properties of the bait

Bait size

Fish feeding in a habitat with a mixture of natural prey of different sizes will often show a preference for a certain prey size (Bjordal and Løkkeborg 1996). Bait size has been shown to have a significant influence on both size selectivity and catching efficiency in longlining for cod and haddock (Engås and Løkkeborg 1994; Johannessen et al. 1993). Johannessen (1983) showed that the size-selection effect was most pronounced in cod, in that larger baits caught only a few small cod, while small and large baits caught approximately the same number of large fish. The same tendency was demonstrated in haddock, but the size-selection effect was less pronounced in this species as larger baits also caught some small haddock.

This difference between cod and haddock may be related to their different responses to baited hooks (Bjordal and Løkkeborg 1996). Haddock usually nibble small pieces of the bait while the rest of the bait and hook are outside the mouth. As haddock often make several attacks on the same bait, the bait becomes smaller and the fish may finally bite the hook and be caught. This behaviour explains why the size-selection effect of bait size is less pronounced in haddock, and also why smaller baits are more efficient than large baits. Cod, on the other hand, suck the whole bait into their mouth, and small cod do not respond to or attack larger baits (Bjordal and Løkkeborg 1996). This difference in responses to longline baits can be explained by differences in natural foraging behaviour, with haddock generally feeding on small stationary benthic organisms and cod on mobile prey, which demand more vigorous responses (Løkkeborg et al. 1989).

Reducing the proportion of small fish in longline catches by increasing bait size will increase total bait consumption. Because bait prices have greatly increased in the course of the past decade, this strategy would lead to a significant increase in bait costs. An alternative solution to this problem has been sought by using an inedible body on the longline hooks (Løkkeborg and Bjordal 1995). Hooks with a plastic body attached and baited with mackerel caught a lower proportion of undersized haddock than hooks with mackerel bait only. In the development of alternative bait types, we need to consider ways of increasing bait size without increasing costs.

Shape, texture and physical strength

Once the fish has encountered the baited hook, the shape of the bait may also affect the likelihood of it attacking and ingesting the bait. Fish show a preference for certain prey types which may be related to the formation of a "search image" (Dawkins 1971; Krebs 1973). The "search image" concept implies that a foraging animal bears an image of the object sought, reacting only to certain diagnostic cues (e.g. shape) that are used in the search (Hart 1986). In a fishing experiment for cod, rectangular shaped shrimp-flavoured artificial baits produced lower catch rates than natural shrimp bait and the difference in catching efficiency was explained in terms of the "search image" concept (Løkkeborg 1990a).

Fish also show a restrained response towards attacking a novel prey item. Three-spined sticklebacks (*Gasterosteus aculeatus*) and rainbow trout exposed to a new prey species required several exposures before they approached the novel prey (Beukema 1968; Ware 1971). Similarly, field observations of cod showed that only 5 % of individuals approached mackerel baits, which can be regarded as a novel prey (i.e. the baits were cut in pieces) (Løkkeborg et al. 1989). The shape of the bait is thus a parameter to be considered in efforts to develop new baits.

Some species use texture to elicit ingestion, thereby sorting prey items from less palatable or inedible objects (Atema 1980). Cod feeding on bivalves were seen to make a series of rapid movements of the head as they tried to shake mussels out of their shells (Brawn 1969). Thus after initially having ingested the bait, fish may spit it out of the mouth due to its unpleasant texture. Comparing natural squid bait with squid bait put in a nylon bag (Løkkeborg 1991) gave reduced catch rates for cod and haddock, and this

effect was explained by the more limited swallowing responses caused by the texture of the nylon bag.

In addition to its chemical and visual properties, the efficiency of a longline bait is determined by its physical strength and ability to remain on the hook throughout the soak period (Bjordal and Løkkeborg 1996). Squid is regarded as an efficient bait for catching cod, possibly due in part to its physical strength. Among the factors that may cause loss of bait are the line-setting process, seabirds, benthic scavengers and target fish taking the bait without getting hooked. A reinforcement may be incorporated into an alternative bait in order to reduce losses, but may have a negative effect on catching efficiency.

Insights from recreational angling

Recreational angling (rod and line fishing) shares many common features with commercial longlining. However, in contrast to commercial fishing, the preferred gears (i.e. type of line, hooks, baits and other attractors) and methods chosen by recreational anglers are often based on beliefs rather than scientific testing. The desire to capture specific targets (both in terms of species and size) may have led to a convergence of efficient selective fishing gears and methods in recreational angling. Thus, commercial longlining has the potential to learn a great deal from recreational angling methods.

The bait type used, its presentation and the odour dispersion often differ between recreational angling and longline fishing. Thus, even though chemoreception is not gear-specific by nature, the differences in bait characteristics and presentation may lead to behavioural differences exhibited by the target species. Although bait renewal is usually more frequent in angling, leading to a potentially more potent odour plume, the total number of baits in use at any one time is much lower, leading to lower spatial coverage. Moreover, soak time is usually much shorter, leading to a lower temporal coverage, and the odour plume will be interrupted in time and space every time the bait is renewed. To counteract these disadvantages, anglers have developed several gear modifications and often use light, prey mimics, additional chemicals, motion and sound to increase the bait's attractiveness. Commercial fishermen seldom use additional cues on their demersal longlines, and so if they adopted some

of these modifications, they could potentially increase their catch rates.

Artificial light is known to attract prey as well as fish, and light has been used to attract fish for thousands of years and is still used in pelagic fisheries (Ben-Yami 1976; Gabriel et al. 2005). A recent laboratory study showed that the nocturnal ringtail cardinalfish (*Apogon annularis*) was more attracted to zooplankton which had fed on luminescent bacteria and subsequently started to glow (Zarubin et al. 2012). A field study found catch rates that were 1.2 times as high in tuna, and up to 4.8 times as high in several bottom-dwelling species when a bait dipped in a luminescent solution was used (Makiguchi et al. 1980). However, this study also showed that the luminescent bait repelled some species such as the striped beakperch (*Oplegnathus fasciatus*).

Luminescent aids are available as (1) chemiluminescent lightsticks, (2) phosphorescent tubes, beads, paint and dips (known as "glow-in-the-dark") which are drawn up the leader, applied to the hook or directly applied to the bait, and (3) fluorescent tubes, beads and paint. Although not as wide-spread as luminescent aids other light-emitting aids, such as battery powered lights, are also used. These lights may be more intense than luminescent aids, but are more expensive and are prone to be replaced more often.

Luminescent material is often used by recreational anglers, and many anglers are convinced of its positive effects on catch rates. However, these beliefs remain to be confirmed via controlled studies. For demersal longlining, no known application has come to our knowledge, although in pelagic longlining chemical light sticks are already widely used to encourage swordfish (*Xiphias gladius*) to ingest the baited hook (Hazin et al. 2005). Dips, tubes and beads for the bait, hook or gangion would be easy to test and be most feasible to implement, but power-driven lights to draw attention to the longline itself could also prove to be effective.

Many anglers use lures that mimic prey fish in combination with baits. Although this would probably be difficult to implement in commercial longlining, the fact that the lure both smells and looks like something edible, could be important. Due to the inherent practical limitations of using lures equipped with an internal hook on commercial longlines, these are not covered in this review. However, presoaked soft bait such as "Gulp" (www.berkley-fishing.com,

22.04.2013) could potentially be fed through automatic baiting machines. Attractants available either as liquid sprays or dips, would also be easy to implement.

Another interesting feature of recreational angling is that baits are often kept in motion while fishing. Sometimes the baits are mounted or fished off-bottom on a beam, and spinners are widely used on fishing tackle to create additional visual effects. However, attempts on lifting longline baits off the bottom have been only partly successful, and more research is needed. For example, Bjordal (1984) tested different types of gangion floats that reduced bait loss, although contradictory results on catch rates were observed. In addition, behavioural observations showed that tusk (*Bromse brosme*) and haddock attacked the float instead of the bait. Developing an alternative bait that is buoyant would eliminate the need for floats and avoid this problem.

Feeding attractants, chemosensory thresholds and feed ingredients

Feeding attractants

Many studies have attempted to identify the chemical nature of feeding attractants and stimulants (see review by Hara 1992; Kasumyan and Døving 2003; Hara 2011). These studies have demonstrated that feeding behaviour in fish is stimulated by low-molecular weight substances with high aqueous solubility including amino acids, peptides, prostaglandins, bile acids and steroids (Carr and Derby 1986; Hara 1992, 2011). Amino acids comprise the most important group, and short-chain neutral amino acids appear to be most stimulating (see review by Hara 1992; 2011; Marui and Caprio 1992; Kasumyan and Døving 2003). They may act either singly or in combination to play a major role in stimulating feeding behaviour (Hara 2011), and the ability of fish to discriminate among different amino acids seems to be very high (Friedrich 2006).

Nearly all studies of chemically stimulated feeding behaviour have shown that food extracts lose their stimulatory effects when their amino acids have been eliminated (Carr and Derby 1986). Each fish species selectively responds to a specific mixture of compounds, but synthetic mixtures of amino acids seldom attain the effectiveness of the extracts from natural foods (Carr and Derby 1986; Ellingsen and Døving 1986; Jones 1992; Hara 2011). Evidence from most of species studied indicates that feeding preferences exhibit some degree of plasticity, which implies some degree of learning.

Studies testing squid extracts on various fish species have shown that the feeding attractants were different for turbot (*Scophthalmus maximus*), rainbow trout and plaice (*Pleuronectes platessa*) (Adron and Mackie 1978; Mackie 1982). The taste responses evoked by common free amino acids were investigated in 21 fish species, and the number of amino acids that acted as stimulants ranged from 0 to 13 (Kasumyan 1997). Alanine, cysteine, serine, glutamine and glycine seemed to be the most important stimulants for these species. Field studies also showed that different species of marine fish were attracted by different mixtures of amino acids (Sutterlin 1975; Kasumyan and Døving 2003).

Studies have also attempted to identify the primary stimuli that elicit food search in cod. Bottom food search behaviour showed that glycine was the most potent single component in shrimp, followed by alanine (Ellingsen and Døving 1986). There was a synergistic effect among glycine, alanine, proline and arginine, and a mixture of these was more effective than the total amino acid mixture in the natural shrimp extract. Laboratory studies designed to identify the active compounds in squid confirmed that amino acids were the major stimulants for cod (Johnstone and Mackie 1990).

Experiments in commercial longlining and anecdotal evidence from fishermen have shown species-selective effects of baits. Fishing trials showed that squid was found to be the most effective bait for cod and hake (*Merluccius* sp.), while mackerel appeared to be more effective for haddock (Martin and McCracken 1954). Bjordal (1983) found that squid bait caught twice as many ling (*Molva molva*) as mackerel but only 9 % more tusk. Comprehensive Japanese studies have demonstrated the species-specific effects of bait type on captures of tuna and marlin (Shimada and Tsurudome 1971; Imai 1972; Imai and Shirakawa 1972). Experiments with artificial baits have also demonstrated effects of bait types on species selectivity (e.g. Yamaguchi et al. 1983; Løkkeborg 1991; Pol et al. 2008). Thus several studies demonstrate that there is great potential for using baits or extract mixtures to attract specific target species to an odour

source. These properties of feeding attractants should form the basis for the development of species-selective bait-fishing methods.

Chemosensory thresholds

The chemosensory detection threshold is the lowest concentration of a given attractant that an animal is capable of detecting. Detection thresholds have been determined for several freshwater and marine fish species (summarized in Løkkeborg et al. 2010). In the study of fish behaviour vis-à-vis baited longlines, however, the response threshold is of greater interest. This threshold determines the concentration of attractants at which the animal responds to the stimulus and searches for the odour source. The distance over which an odour source attracts fish is determined by the initial release rate of the attractants, the rate of dilution (i.e. turbulence) as the odour plume is dispersed by the current, and the chemosensory response threshold of the target fish.

Although response thresholds are more relevant than detection thresholds for various behavioural aspects of food search, few studies have been carried out to determine response thresholds. Behavioural response thresholds to an extract of squid bait have been studied in sablefish kept on three different feeding regimes (Løkkeborg et al. 1995). The response threshold to total dissolved free amino acids (DFAAs) in fish fed to satiation was 4.4×10^{-8} M, while the threshold in fish tested after four days of food deprivation was determined to be as low as 1.4×10^{-11} M, i.e. 3,000 times lower. Response thresholds to glycine were estimated to be less than 10^{-7} M in cod and whiting (Pawson 1977).

Feed ingredients that stimulate feed intake

The inclusion in feed formulations of ingredients that act as stimulants is common in aquaculture. For example, dietary addition of extracts from tissues of common prey organisms such as squid, shrimp, mussels and krill have been reported to stimulate consumption in a range of marine species (Mackie et al. 1980; Tandler et al. 1982; Mackie and Mitchell 1983; Mearns et al. 1987; Ikeda et al. 1988a, b; Fukuda et al. 1989; Johnstone and Mackie 1990; Kamstra and Heinsbroek 1991; Toften 1997).

The amino acids alanine, cysteine, serine, glutamine, glycine and proline seem to act as feeding stimulants, either separately or when included in a mixture (Raubenhaimer et al. 2010). Betaine is found in many prey species and is a feeding stimulant for several fish species, including some flatfish, salmonids and sturgeons (Mackie and Mitchell 1985; Kasumyan and Døving 2003; Yamashita et al. 2006). Nucleosides and their derivatives have been shown to stimulate feed intake in some species of flatfish (Raubenhaimer et al. 2010). Fatty acid oxidation products and their derivatives may stimulate feeding at low concentrations (Jobling 2004). Studies have shown that fish fed with diets supplemented with whole extracts display higher rates of feeding than fish fed with diets containing only certain fractions of the extracts or single chemicals (Adron and Mackie 1978; Mackie and Adron 1978; Mackie et al. 1980; Ikeda et al. 1988a, b; Johnstone and Mackie 1990; Takaoka et al. 1990; Hara 2011). In some cases, however, certain mixtures or chemicals can produce similar feeding responses to whole extracts (Adron and Mackie 1978; Mackie and Adron 1978; Ohsugi et al. 1978; Mackie et al. 1980; Fukuda et al. 1989).

The ability of fish to select nutritionally appropriate diets based on previous experience has been demonstrated in studies of macronutrient self-selection (Raubenhaimer et al. 2010). It has been shown that fish species that were offered separate diets, each with a single macronutrient (protein, lipids and carbohydrate), chose a diet that reflected their natural feed habitat (Sánchez-Vázquez et al. 1999; Aranda et al. 2000). The macronutrients selected may vary over the season, for example sea bass (*Dicentrarchus labrax*) favoured a protein-rich diet in the spring, but selected a more lipid-rich diet in late summer (Rubio et al. 2008; Raubenhaimer et al. 2010).

An overview of efforts to develop alternative longline baits

Efforts to develop alternative longline baits to replace traditional bait types have been made in several countries for many years, mostly with limited success (e.g. Bjordal and Løkkeborg 1996; Januma et al. 2003; Pol et al. 2008; Henriksen 2009). Two main methods to develop an alternative or artificial longline bait have been tried; one based on natural resources (e.g. surplus products from the fishing industry) and the other on synthetic ingredients (chemicals) as attractants. In

Table 2 Overview of alternative longline baits and their main constituents

Name	Producer	Main attractants	Binder	Reinforcement
Norbait	Nortbait DA	Minced surplus products	Alginate	Cotton stocking
Artificial bait	William E.S. Carr	Any liquefied attractant	Polyurethane foam	Fabric substrate
Bait bags	Bernskan ehf.	Frozen fish or surplus products	*	Cellulose fibre
Arom Bait	Arom Bait	*	*	*

* Information unavailable or not applicable

both cases, the bait is based on three main components: attractants, binder (gelling agent) and reinforcement. All these components must meet important requirements if they are to form an efficient longline bait. The attractants, whether natural or synthetic, must include the stimulatory compounds that elicit the food-search behaviour in the target fish species. The purpose of the binder is to ensure that attractants are released over a fairly long period of time (i.e. several hours). The release rate of attractants from natural baits have been shown to decrease very rapidly (Løkkeborg 1990b), and although this has not been demonstrated experimentally, it is likely that baits with prolonged release rates would increase catch rates. Finally, as the binder (gelling agent) normally does not add sufficient physical strength to the bait, a reinforcement is needed to ensure that bait is not lost, either during line shooting, or to sea birds, benthic bait scavengers or the target species. Table 2 summarizes current manufacturers of alternative longline baits.

Norbait

This bait type, manufactured by the Norwegian company Norbait DA, is based on surplus products (e.g. waste fish and fish offal) from the fish-processing industry (www.norbait.com, 22.04.2013). Alginate is used as gelling agent, and a cotton stocking as reinforcement. The technology used to manufacture the Norbait bait is similar to that used for production of sausages. Minced fish products are mixed with the gelling agents and the mixture is then extruded into a fibre mesh tube (stocking) to form a long "sausage". This production technology makes a very suitable bait for baiting machines. The production of Norbait is patented worldwide.

Baits based on several types of surplus products (e.g. herring, mackerel, horse mackerel) have been developed, and species-selective effects have been demonstrated in fishing trials. Increases in catch rates of two to three hundred per cent compared with natural bait have been obtained for haddock, although Norbait compared poorly for cod. A similar type of bait that uses different gelling agents (guar gum or fish skin collagen) has been tested in fishing trials for tusk, ling, cod and haddock (Løkkeborg 1991). Compared to natural bait, minced herring enclosed in a nylon bag resulted in a 58 % higher catch rates for haddock, a non-significant catch increase for tusk and ling, and a considerably lower catch rate for cod.

Artificial bait invented by William E.S. Carr

This bait comprises a water-insoluble, hydrophilic matrix (a polyurethane foam) which is permeable (by diffusion) to the release of attractants incorporated into the matrix (http://freepatentsonline.com/4245420.html, 22.04.2013). On immersion in water the attractants are released at a predetermined rate over a prolonged period of time. The matrix comprises the solid phase of a colloidal solution of a liquid in a macromolecular substance. The attractants are incorporated into the matrix by inclusion in the colloidal solution prior to the formation of the solid phase. The matrix is a semi-rigid and flexible material that in texture resembles common fish prey. A reinforcing substrate (e.g. a fabric) is incorporated into the matrix to provide physical strength. Any fish attractants in liquid form can be incorporated in this artificial bait, e.g. liquefied marine products, fish oil or synthetic attractants. Useful attractant mixtures that can be tailored for specific target species are described by the inventor of this artificial bait (Carr and Derby 1986; Carr et al. 1996).

This artificial bait impregnated with feeding attractants that occur in natural shrimp bait has been tested in the spring fishery for cod off the coast of northern Norway (Løkkeborg 1990a). Three sizes of

the bait were tested, and the small artificial bait produced similar catch rates to that of natural shrimp bait, while the two larger sizes compared poorly. Fewer small cod were caught on the artificial baits, while there was no difference in the number of large cod caught on artificial and natural shrimp baits. This size-selective effect was explained by different preferences regarding prey species and prey size between small and large cod (Løkkeborg 1990a).

Bait bags

The "bait bags" are produced by the Icelandic company Bernskan ehf (Sudavik, Iceland) (Henriksen 2009). This bait is based on frozen natural raw material such as capelin, herring, sand eel, squid, extract from Calanus species and mixtures of fish waste products. The frozen raw material is set together under high pressure before being injected into small cellulose fibre bags containing an average of 10 g of bait per bag. In field experiments in Norway, the bait bags were compared with saury and mackerel baits, and the bags produced a higher catch rate of haddock, but poorer catches of cod (Henriksen 2009). The bait bags have also been tested in deep-water (300–400 m) longline fishing for halibut with limited success (Edgard Henriksen, Nofima AS, personal communication). However, the bait bags have several advantages for fishermen using traditional hand-baited longlines, including the elimination of the need to cut the bait, cleanliness, a rapid baiting process, and reduced hook entanglements during setting. Another advantage is that seabirds showed no interest in the bags, thus mitigating the seabird bycatch problem (Henriksen 2009).

Arom Bait

This artificial bait is manufactured by the Spanish company Arom Bait. The bait is made from natural and biodegradable products, and is moulded into rectangular and flexible boards that can be cut into suitably sized pieces. Bait types have been developed for both longlining and recreational angling. This product can be stored without freezing. The manufacturer has patented its products and little information on its chemical composition and catching efficiency exists (www.arombait.com, 22.04.2013).

Other artificial baits

Other examples of artificial baits include a latex and vinyl chloride artificial bait that was developed in order to eliminate the need to freeze bait on Japanese tuna longliners (Koyama 1956; Turudome 1970; Januma et al. 2003). Liver of squid was used as the main attractant and combined with seaweed products. The bait was reinforced with gauze and formed into a simple rectangular shape. The catch rate of the artificial bait was lower than that of natural baits, which may have been partly due to neglecting the importance of the shape of the bait (Januma et al. 2003).

There are also reports of artificial baits whose the ingredients and binders are secret (Erickson et al. 2000; Erickson and Berkeley 2008). These studies tested species-selective artificial baits for the Alaskan demersal longline fishery. The fabricated baits fished as well as or better than herring for sablefish and Pacific halibut, while reducing bycatch of spiny dogfish shark (*Squalus acanthias*), skate (*Raja* spp.), arrowtooth flounder (*Atheresthes stomias*) and Pacific cod (*Gadus macrocephalus*) by more than an order of magnitude.

Several new industry-driven initiatives on developing artificial baits for longline fishing are under way in Norway. The Tromsø-based company Polybait AS is running a project with financial support from the Research Council of Norway. Their bait is based on polymer composites in combination with natural attractants (Svein Kvalvik, Polybait AS, personal communication). Another Norwegian industry-driven project is based on the use of extruded starch as binder (patent number NO-309961; Anfinn Sjåstad, personal communication). Preliminary studies with pots have been carried out to test potential attractants to be incorporated into the starch binder. Promising results were obtained for Norway lobster (*Nephrops norvegicus*), while catch rates for fish were low (author's unpublished data). These Norwegian initiatives reflect the high prices of traditional baits and the demands for stable supplies of bait.

Conclusion and recommendations

This review has shown that there exists a large quantity of important knowledge about fish behaviour

and fish sensory modalities that are essential for future efforts to develop alternative longline baits. To date, these efforts have generally not been successful, and to the best of our knowledge, only natural and traditional baits are currently used by commercial longline vessels although recreational anglers have started to use alternative baits. However, as the demand for marine resources for human consumption grows, longline bait costs are likely to continue to increase. The development of alternative baits based on resources not used for human consumption may therefore prove to be critical to viable longline fisheries.

Species specificity is a common feature of food search behaviour. The chemical compounds that elicit olfactory search and trigger gustatory food ingestion differ among species. Thus there is a great potential for improved species selectivity in longline fishing by incorporating species-specific attractants in manufactured baits. However, more research is needed to identify the feeding attractants for important target species to develop species-specific baits.

Furthermore, longline efficiency could be improved by taking the unique properties of a chemical stimulus into account and develop a long-lasting bait that attracts fish from a large area over a long period of time. Here, more knowledge of chemosensory response thresholds in target species and a better understanding of odour plume dispersal under changing current conditions are of great importance. Pharmacological and chemical expertise is also needed to identify suitable gelling agents to be incorporated in a long-lasting bait.

Although underwater vision has a short range, it is important for bait acceptance and to trigger bait attacks. Several factors affect visual detection, and efforts to develop more efficient baits should focus on contrast, colour and movement. Manufactured baits may be made more visible than natural baits by increasing contrast and using fluorescent colours or polarising coatings. If baits are made buoyant, they will move with the current and become more visible. A moving object will also facilitate bait location mediated by the mechanosensory system. Furthermore, movement triggers fish to attack a prey, while floating the baits off the bottom will decrease bait losses to benthic scavengers.

Factors related to physical properties can easily be manipulated in an alternative bait. Different species (e.g. cod and haddock) show different responses to changes in bait size. Baits of different sizes but with similar attractant release rates could thus be manufactured to target different species. Although knowledge of the effects of bait shape is sparse, baits that mimic natural prey items are probably more efficient than baits whose shape is unfamiliar to the fish. Even less is known about the effects of bait texture, but baits whose textures imitate the textures of natural prey are more likely to trigger bait ingestion. Finally, baits that withstand bait loss and stay on the hook throughout the soak period can be made by using gelling agents and reinforcements of appropriate strength. Reinforcements affect texture and may have a negative impact on acceptance and ingestion; however, this problem can be mitigated by integrating the reinforcement material into a bait matrix whose texture resembles that of common prey items.

Visibility, shape and texture may prove to have great effects on the likelihood of fish to attack and ingest bait. As very little is known about how these visual and physical properties of the bait affect fish behaviour, such studies should be given priority in future efforts to develop alternative baits.

Feeding motivation and food search behaviour are affected by a wide range of internal (hunger state, life history) and external (time of day, season, temperature, current) factors (Fig. 1; Table 1). The outcome of longline fishing therefore depends on when, where and how the gear is deployed. For example, setting baited longlines at sunrise/sunset, at moderate tides, across-current and in areas or seasons of low prey density (i.e. hungry target fish) is likely to increase catch efficiency. Although they are not specific to longlines baited with artificial baits, these behavioural aspects ought to be taken into account in longline fishing.

In summary, this review has revealed that few studies have been aimed at developing new bait types to replace traditional longline baits. Moreover, the studies that do exist provide little information about the composition and preparation of the baits tested. On the other hand, studies on longlining in general and on various aspects of food search behaviour are numerous. These have greatly improved our understanding of how fish respond to baited gear, and this knowledge is of paramount importance for future research aimed at the development of alternative baits and for efforts to improve longline fishing in general.

References

Adamek Z, Fasaic K, Debeljak L (1990) Lower temperature limits of plant food intake in young grass carp (*Ctenopharyngodon idella*, Val). Ichthyol 22:1–8

Adron JW, Mackie AM (1978) Studies on the chemical nature of feeding stimulants for rainbow trout, (*Salmo gairdneri*, Richardson). J Fish Biol 12:303–310

Aranda A, Sánchez-Vázquez FJ, Zamora S, Madrid JA (2000) Self-design of fish diets by means of self-feeders: validation of procedures. J Physiol Biochem 56:155–166

Atema J (1980) Chemical senses, chemical signals and feeding behavior in fishes. In: Bardach JE, Magnuson JJ, May RC, Reinhart JM (eds) Fish behavior and its use in the capture and culture of fishes. International Centre for Living Aquatic Resources Management, Manila, pp 57–101

Baker CF, Montgomery JC (1999) The sensory basis of rheotaxis in the blind Mexican cave fish, *Astyanax fasciatus*. J Comp Physiol A 184:519–527

Baker CF, Montgomery JC, Dennis TE (2002) The sensory basis of olfactory search behavior in banded kokopu (*Galaxias fasciatus*). J Comp Physiol A 188:553–560

Ben-Yami M (1976) Fishing with light. By arrangement with the Food and Agriculture Organization of the United Nations by Fishing News Books, Farnham

Bertrand A, Josse E, Bach P, Gros P, Dagorn L (2002) Hydrological and trophic characteristics of tuna habitat: consequences on tuna distribution and longline catchability. Can J Fish Aquat Sci 59:1002–1013

Beukema JJ (1968) Predation by the three-spined stickleback (*Gasterosteus aculeatus* L.): the influence of hunger and experience. Behaviour 31:1–126

Bjordal A (1983) Effect of different long-line baits (mackerel, squid) on catch rates and selectivity for tusk and ling. ICES CM/B:31

Bjordal A (1984) The effect of gangion floats on bait-loss and catch rates in longlining. ICES CM/B:8

Bjordal A, Løkkeborg S (1996) Longlining. Fishing News Books, Oxford, p 156

Brawn VM (1969) Feeding behaviour of Cod (*Gadus morhua*). J Fish Res Board Can 26:583–596

Breck JE, Gitter MJ (1983) Effect of fish size on the reactive distance of bluegill (*Lepomis macrochirus*) sunfish. Can J Fish Aquat Sci 40:162–167

Brett JR (1979) Environmental factors and growth. In: Hoar WS, Randall DJ, Brett JR (eds) Fish physiology, vol VIII., Bioenergetics and growthAcademic press, New York and London, pp 599–675

Carr WES, Derby CD (1986) Chemically stimulated feeding behavior in marine animals. J Chem Ecol 12:989–1011

Carr WES, Netherton JC III, Gleeson RA, Derby CD (1996) Stimulants of feeding behaviour in fish: analysis of tissue of diverse marine organisms. Biol Bull 190:149–160

Carton AG, Montgomery JC (2003) Evidence of a rheotactic component in the odour search behaviour of freshwater eels. J Fish Biol 62:501–516

Castonguay M, Cyr DG (1998) Effects on temperature on spontaneous and thyroxine-stimulated locomotor activity of Atlantic cod. J Fish Biol 53:303–313

Confer JL, Howick GL, Corzett MH, Kramer SL, Fitzgibbon S, Landesberg R (1978) Visual predation by planktivorous. Oikos 31:27–37

Cronin TW, Shashar N (2001) The linearly polarized light field in clear, tropical marine waters: spatial and temporal variation of light intensity, degree of polarization and e-vector angle. J Exp Biol 204:2461–2467

Crowl TA (1989) Effects of crayfish size, orientation, and movement on the reaction distance of largemouth bass foraging in clear and turbid water. Hydrobiology 183:133–140

Dawkins M (1971) Perceptual changes in chicks: another look at the "search image" concept. Anim Behav 19:566–574

Denton EJ, Warren FJ (1956) Visual pigments of deep-sea fish. Nature 178:1059

Easter SS, Johns PR, Baumann L (1977) Growth of the adult goldfish eye. I. Optics. Vis Res 16:469–476

Ellingsen OF, Døving KB (1986) Chemical fractionation of shrimp extracts inducing bottom food search behavior in cod (*Gadus morhua* L.). J Chem Ecol 12:155–168

Engås A, Løkkeborg S (1994) Abundance estimation using bottom gillnet and longline-the role of fish behavior. In: Fernö A, Olsen S (eds) Marine fish behaviour in capture and abundance estimation. Fishing News Books, Oxford, pp 134–165

Erickson DL, Berkeley S (2008) Methods to reduce by catch mortality in longline fisheries. In: Camhi M, Pikitch EK, Babcock EA (eds) Sharks of the open ocean—biology, fisheries and conservation. Blackwell Publishing, Oxford, pp 462–471

Erickson D, Goldhor S, Giurca R (2000) Efficiency and species selectivity of fabricated baits used in Alaska demersal longline fisheries. ICES CM 2000/J:04

Eriksson L-O (1978) Nocturnalism versus diurnalism—dualism within fish individuals. In: Thorpe JE (ed) Rhythmic activity of fishes. Academic Press, London, pp 69–89

Fernö A, Solemdal P, Tilseth S (1986) Field studies on the behavior of whiting (*Gadus merlangus* L.) toward baited hooks. Fiskeridirektoratets Skrifter Serie Havundersøkelser 18:83–95

Flamerique IN, Browman HI (2001) Foraging and prey-search behaviour of small juvenile rainbow trout (*Oncorhynichus mykiss*) under polarized light. J Exp Biol 204:2415–2422

Fraser NHC, Metcalfe NB, Thorp JE (1993) Temperature depended switch between diurnal and nocturnal foraging in salmon. Proc R Soc 252B:135–139

Friedrich RW (2006) Mechanisms of odor discrimination: neurophysiological and behavioral approaches. Trends Neurosci 29:40–47

Fukuda K, Kohbara J, Zeng C, Hidaka I (1989) The feeding—stimulatory effects of squid muscle extracts on the young yellowtail *Serioal quinqueradiata*. Nippon Suisan Gakkaishi 55:791–797

Gabriel O, Lange K, Dahm E, Wendt T (2005) Von Brandt's fish catching methods of the world. Blackwell, Oxford

Gibson RN (1992) Tidally synchronised behavior in marine fishes. In: Ali MA (ed) Rhythms in fishes. Plenum Press, New York, pp 63–82

Gregory RS, Northcote TG (1993) Surface, planktonic, and benthic foraging by juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in turbid laboratory conditions. Can J Fish Aquat Sci 50:233–240

Guthrie DM, Muntz WRA (1993) Role of vision in fish behaviour. In: Pitcher TP (ed) Behaviour of teleost fishes, 2nd edn. Chapman & Hall, London, pp 89–121

Hairston NG, Li KT, Easter SS (1982) Fish vision and the detection of planktonic prey. Science 218:1240–1242

Hara TJ (1992) Overview and introduction. In: Hara TJ (ed) Fish chemoreception. Fish and fisheries series 6. Chapman & Hall, London, pp 1–12

Hara TJ (1994) Olfaction and gustation in fish: an overview. Acta Physiol Scand 152(2):207–217

Hara TJ (2011) Smell, taste and chemical sensing. In: Farrell AP (ed) Encyclopedia of fish physiology: from genom to environment, vol 1. Academic Press/Elsevier, London/Amsterdam, pp 183–235

Hart PJB (1986) Foraging in teleost fishes. In: Pitcher TJ (ed) The behaviour of teleost fishes. Croom Helm, London, pp 211–236

Hart PJB, Connellan B (1984) The cost of prey capture, growth rate and ration size in pike (*Esox lucius*) as functions of prey weight. J Fish Biol 25:279–291

Hawkins AD (1986) Underwater sound and fish behaviour. In: Pitcher TJ (ed) The behaviour of teleost fishes. Croom Helm, London, pp 114–151

Hazin H, Hazin F, Travassos P, Erzini K (2005) Effect of lightsticks and electralume attractors on surface-longline catches of swordfish (*Xiphias gladius*, Linnaeus, 1959) in the southwest equatorial Atlantic. Fish Res 72:271–277

Heller R, Milinski M (1979) Optimal foraging of sticklebacks on swarming prey. Anim Behav 27:1127–1141

Hemmings CC (1965) Factors influencing the visibility of objects under water. In: Bainbridge R, Evans GC, Rackham O (eds) Light as an ecological factor. Blackwell, Oxford, pp 359–374

Henriksen E (2009) Det egner seg! Nofima report no. 28/2009 (in Norwegian)

Higgins PJ, Talbot C (1985) Growth and feed intake in juvenile Atlantic salmon (*Salmo salar* L.). In: Cower CB, Mackie AM, Bell JG (eds) Nutrition and feeding in fish. Academic Press, London, pp 243–263

Hino H, Miles NG, Bandoh H, Ueda H (2009) Molecular biological research on olfactory chemoreception in fishes. J Fish Biol 75:945–959

Holmes RA, Gibson RN (1986) Visual cues determining prey by the turbot, (*Scophthalmus maximus* L.). J Fish Biol 29:49–58

Houlihan D, Boujard T, Jobling M (2001) Food intake in fish. Blackwell, Oxford

Howick GL, O'Brien WJ (1983) Piscivorous feeding behaviour of largemouth bass: an experimental analysis. Trans Am Fish Soc 112:508–516

Ikeda I, Hosokawa H, Shimeno S, Takeda M (1988a) Identification of feeding stimulant for jack mackerel in its muscle extract. Bull Jpn Soc Sci Fish 54:229–233

Ikeda I, Hosokawa H, Shimeno S, Takeda M (1988b) Identification of feeding stimulant in the krill extract for jack mackerel. Bull Jpn Soc Sci Fish 54:235–238

Imai T (1972) Studies on the several raw fish baits in a tuna longline. Fishing-I. Mem Fac Fish Kagoshima Univ 21:45–50

Imai T, Shirakawa O (1972) Studies on the several raw fish baits in tuna long-line. Fishing-H. Mem Fac Fish Kagoshima Univ 21:51–62

Ishida Y, Kobayashi H (1992) Stimulatory effectiveness of amino acids on the olfactory response in an algivorous marine teleost, the rabbitfish *Siganus fuscescens* Houttuyn. J Fish Biol 41:737–748

Januma S, Miyajima K, Abe T (2003) Development and comparative test of squid liver artificial bait for tuna longline. Fish Sci 69:288–292

Jerlov NG (1968) Optical oceanography. Elsevier, Amsterdam, p 194

Jobling M (1994) Fish bioenergetics. Chapman & Hall, London, p 309

Jobling M (2004) On-growing to market size. In: Moksness E, Kjørsvik E, Olsen Y (eds) Culture of cold-water marine fish. Blackwell, Oxford, pp 363–432

Jobling M, Alanärä A, Noble C, Sanchez-Vazquez J, Kadri S, Huntingford F (2010) Appetite and feeding. In: Huntingford F, Jobling M, Kadri S (eds) Aquaculture and behavior. Wiley, Oxford, pp 183–219

Johannessen T (1983) Influence of hook and bait size on catch efficiency and length selection in longlining for cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus* L.). MSc Thesis, University of Bergen, Norway (in Norwegian)

Johannessen T, Fernö A, Løkkeborg S (1993) Behaviour of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) in relation to various sizes of long-line bait. ICES Mar Sci Symp 196:47–50

Johnstone ADF (1980) The detection of dissolved amino acids by the Atlantic cod, (*Gadus morhua* L.). J Fish Biol 17:219–230

Johnstone ADF, Mackie AM (1990) Laboratory investigations of bait acceptance by the cod, (*Gadus morhua* L.): identification of feeding stimulants. Fish Res 9:219–230

Jones KA (1992) Food search behavior in fish and the use of chemical lures in commercial and sports fishing. In: Hara TJ (ed) Fish chemoreception. Chapman & Hall, London, pp 288–320

Jørgensen EH, Jobling M (1989) Patterns of food intake in Arctic charr, (*Salvelinus alpinus*, L.), monitored by radiography. Aquaculture 81:155–160

Jørgensen EH, Johansen SJS, Jobling M (1997) Seasonal patterns of growth, lipid, deposition and lipid depletion in anadromous Arctic charr. J Fish Biol 51:312–326

Kalmijn AJ (1988) Hydrodynamic and acoustic field detection. In: Atema J, Fay RR, Popper AN, Tavolga WN (eds) Sensory biology of aquatic animals. Springer, New York, pp 83–130

Kamermans M, Hawryshyn C (2011) Teleost polarization vision: how it might work and what it might be good for. Philos Trans R Soc B 366:742–756

Kamstra A, Heinsbroek LTN (1991) Effects of attractants on start of feeding of glass eel, (*Anguilla anguilla* L.). Aquac Res 22:47–56

Karas P (1990) Seasonal changes in growth and standard metabolic rate of juvenile perch, *Perca fluviatilis* L. J Fish Biol 37:913–920

Kasumyan AO (1997) Gustatory reception and feeding behavior in fish. J Ichthyol 37:72–86

Kasumyan AO, Døving KB (2003) Taste preferences in fishes. Fish Fish 4:289–347

Komourdjian MP, Saunders RL, Fenwick JC (1976) Evidence for the role of growth hormone as a part of a 'light-pituitary axis' in growth and smoltification of Atlantic salmon (*Salmo salar*). Can J Zool 54:544–551

Koyama T (1956) Study on bait for tuna longline, I. An artificial bait of latex-sponge shaped like a squid. Bull Tokai Reg Fish Res Lab 15:89–94

Krebs JR (1973) Behavioral aspects of predation. In: Bateson PPG, Klopfer PH (eds) Perspectives in ethology, vol 1. Plenum Press, New York, pp 73–111

Kuparinen A, Klefoth T, Arlinghaus R (2010) Abiotic and fishing-related correlates of angling catch rates in pike (*Esox lucius*). Fish Res 105:111–117

Lazzaro X (1987) A review of planktivores fishes: their evolution, feeding behaviours, selectivity and impacts. Hydrobiologia 146:97–167

Leatherland JF, Farbridge KJ, Boujard T (1992) Lunar and semilunar rhythm in fishes. In: Ali MA (ed) Rhythms in fishes. Plenum, New York, pp 83–107

Løkkeborg S (1990a) Reduced catch of under-sized cod (*Gadus morhua*) in longlining by using artificial bait. Can J Fish Aquat Sci 47:1112–1115

Løkkeborg S (1990b) Rate of release of potential feeding attractants from natural and artificial bait. Fish Res 8:253–261

Løkkeborg S (1991) Fishing experiments with an alternative longline bait using surplus fish products. Fish Res 12:43–56

Løkkeborg S (1998) Feeding behavior of cod, (*Gadus morhua*): activity rhythm and chemically mediated food search. Anim Behav 56:371–378

Løkkeborg S, Bjordal A (1995) Size-selective effects of increasing bait size by using an inedible body on longline hooks. Fish Res 24:273–279

Løkkeborg S, Fernö A (1999) Diel activity pattern and food search behavior in cod, *Gadus morhua*. Environ Biol Fish 54:345–353

Løkkeborg S, Pina T (1997) Effects of setting time, setting direction and soak time on longline catch rates. Fish Res 32:213–222

Løkkeborg S, Bjordal Å, Fernö A (1989) Responses of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) to baited hooks in the natural environment. Can J Fish Aquat Sci 46:1478–1483

Løkkeborg S, Olla BL, Pearson WH, Davis MW (1995) Behavioral responses of *sablefish*, (*Anoplopoma fimbria*), to bait odor. J Fish Biol 46:142–155

Løkkeborg S, Fernö A, Humborstad O-B (2010) Fish behavior in relation to longlines. In: He P (ed) Behavior of marine fishes: capture processes and conservation challenges. Wiley, Oxford, pp 105–141

Losey GS, Cronin TW, Goldsmith TH, Hyde D, Marshall NJ, McFarland WN (1999) The UV visual world of fishes: a review. J Fish Biol 54:921–943

Lythgoe JN (1975) The ecology, function and phylogeny of iridescent multilayers in fish corneas. In: Evans GC, Bainbridge R, Rackham O (eds) Light as an ecological factor, 2nd edn. Blackwell, Oxford, pp 211–247

Lythgoe JN (1984) Visual pigments and environmental light. Vis Res 24:1539–1550

Mackie AM (1982) Identification of the gustatory feeding stimulants. In: Hara TJ (ed) Chemoreception in fishes. Elsevier, Amsterdam, pp 275–291

Mackie AM, Adron JW (1978) Identification of inosine and inosine-5′-monophosphate as the gustatory feeding stimulants for the turbot, (*Scophthalmus maximus*). Comp Biochem Physiol 60A:79–83

Mackie AM, Mitchell AI (1983) Studies on the chemical nature of feeding stimulants for the juvenile European eel (*Anguilla anguilla* L.). J Fish Biol 22:425–430

Mackie AM, Mitchell AI (1985) Identification of gustatory feeding stimulants for fish applications in aquaculture. In: Cowey CB, Mackie AM, Bell JG (eds) Nutrition and feeding in fish. Academic Press, London, pp 177–189

Mackie AM, Adron JW, Grant PT (1980) Chemical nature of feeding stimulants for the juvenile Dover sole, *Solea solea* (L.). J Fish Biol 16:701–708

Makiguchi N, Arita M, Asai Y (1980) Application of a luminous bacterium to fish-attracting purpose. Bull Jpn Soc Sci Fish 46:1307–1312

Martin WR, McCracken FD (1954) Relative efficiency of baits for ground fish. Prog Rep Atl Biol Stn 126:17–20

Marui T, Caprio J (1992) Teleost gustation. In: Hara TJ (ed) Fish chemoreception. Chapman & Hall, London, pp 171–198

McFarland WN, Munz FW (1975) Part III: the evolution of photopic visual pigments in fishes. Vis Res 15:1071–1080

McMahon TE, Holanov SH (1995) Foraging success of largemouth bass (*Micropterus salmoides*) at different light intensities: implications for time and depth of feeding. J Fish Biol 46:759–767

Mearns KJ, Ellingsen OF, Døving KB, Helmer S (1987) Feeding behavior in adult rainbow trout and Atlantic salmon parr, elicited by chemical fractions and mixtures of compounds identified in shrimp extract. Aquaculture 64:47–63

Michalsen K, Godø OR, Fernö A (1996) Diel variation in the catchability of gadoids and its influence on the reliability of abundance indices. ICES J Mar Sci 53:389–395

Montgomery J, Coombs S, Halstead M (1995) Biology of the mechanosensory lateral line in fishes. Rev Fish Biol Fish 5:399–416

Montgomery JC, Baker CF, Carton AC (1997) The lateral line can mediate rheotaxis in fish. Nature 389:960–963

Morgan M, Ritz DA (1984) Effect of prey density and hunger states on capture of krill, Nyctiphanes australis Sars, by Australian salmon Arripis trutta. J Fish Biol 24:51–58

Munz FW, McFarland WN (1977) Evolutionary adaptations of fishes to the photic environment. In: Crescitelli F (ed) Handbook of sensory physiology, Vol VII/5, The visual system in vertebrates. Springer, Berlin, pp 193–274

O'Brian WJ, Slade NA, Vinyard GL (1976) Apparent size as the determinant of prey selection by bluegill sunfish (*Lepomis mocochirus*). Ecology 57:1304–1310

Ohsugi T, Hidaka I, Ikeda M (1978) Taste receptor stimulation and feeding behaviour in the puffer, Fugu pardalis. 2. Effects produced by mixtures of constituents of clam extracts. Chem Senses Flavour 3:355–368

Pawson MG (1977) Analysis of a natural chemical attractant for whiting, *Merlangius merlangus* L. and cod, *Gadus morhua*

L. using a behavioural bioassay. Comp Biochem Physiol 56A:129–135

Pearson WH, Miller SE, Olla BL (1980) Chemoreception in the food-searching and feeding behavior of the red hake, (*Urophycis chuss*, Walbaum). J Exp Mar Biol Ecol 48:139–150

Pol MV, Correia SJ, MacKinnon R, Carver J (2008) Longlining haddock with manufactured bait to reduce catch of Atlantic cod in a conservation zone. Fish Res 94:199–205

Raubenhaimer D, Simpson S, Sánchez-Vázquez FJ, Huntingford F, Kadri S, Jobling M (2010) Nutrition and diet choice. In: Huntingford F, Jobling M, Kadri S (eds) Aquaculture and behavior. Wiley, Oxford, pp 150–182

Rimmer DM, Power G (1978) Feeding response of Atlantic salmon (*Salmo salar*) alevins in flowing and still water. J Fish Res Board Can 3:329–332

Rubio VC, Sánchez-Vázquez FJ, Zamora S, Madrid JA (2008) Endogenous modification of macronutrient selection pattern in sea bass (*Dicentrarchus Labrax*, L.). Physiol Behav 95:32–35

Ryer CH, Olla BL (1999) Light-induced changes in the prey consumption and behavior of two juvenile planktivorous fish. Mar Ecol Prog Ser 181:41–51

Sæther B-S, Johnsen HK, Jobling M (1996) Seasonal changes in food consumption and growth of Arctic charr exposed to either simulated natural or a 12:12 LD. photoperiod at constant water temperature. J Fish Biol 48:1113–1122

Sánchez-Vázquez FJ, Yamamoto T, Akiyama T, Madrid JA, Tabata M (1999) Macronutrient self-selection through demand feeders in rainbow trout. Physiol Behav 66:45–51

Scott A (1987) Prey selection by juvenile cyprinids from running water. Freshw Biol 17:129–142

Shashar N, Hagan R, Boal JG, Hanlon RT (2000) Cuttlefish use polarization sensitivity in predation on silvery fish. Vis Res 40:71–75

Shashar N, Johnsen S, Lerner A, Sabbah S, Chiao C-C, Mäthger LM, Hanlon RT (2011) Underwater linear polarization: physical limitations to biological functions. Philos Trans R Soc B 366:649–654

Shimada K, Tsurudome M (1971) On the bait for tuna long-line-IT. On the saury, mackerel and maclcerel scad baits for tuna fishing. Mem Fac Fish Kagoshima Univ 20:119–130

Steingrund P, Clemetsen DH, Mouritsen R (2009) Higher food abundance reduces the catchability of cod (*Gadu morhua*) to longlines on Faroe Plateau. Fish Res 100:230–239

Stoner AW (2003) Hunger and light level alter response to bait by Pacific halibut: laboratory analysis of detection, location and attack. J Fish Biol 62:1176–1193

Stoner AW (2004) Effects of environmental variables on fish feeding ecology: implications for the performance of baited fishing gear and stock assessment. J Fish Biol 65:1445–1471

Stoner AW, Sturm EA (2004) Temperature and hunger mediate sablefish (*Anoplopoma fimbria*) feeding motivation: implications for stock assessment. Can J Fish Aquat Sci 61:238–246

Sutterlin AM (1975) Chemical attraction of some marine fish in their natural habitat. J Fish Res Board Can 32:729–738

Takaoka O, Takii K, Nakamura M, Kumai H, Takeda M (1990) Identification of feeding stimulants for marbled rockfish. Bull Jpn Soc Sci Fish 56:345–351

Tandler A, Berg BA, Kissil GW, Mackie AM (1982) Effect of food attractants on appetite and growth rate of gilthead bream, *Sparus aurata* L. J Fish Biol 20:673–681

Thorpe JE (1978) Rhythmic activity of fishes. Academic Press, London, p 312

Toften H (1997) Oxytetracycline as a feeding deterrent and squid extract as a feed stimulant in salmonid diets. DrSci Thesis, University of Tromsø, Norway

Turudome M (1970) On the bait for tuna longline, I. An artificial bait of vinyl chloride shaped like a flying fish. Mem Fac Fish Kagoshima Univ 19:81–90

Utne ACW (1997) The effect of turbidity and illumination on the reaction distance and search time of the marine planktivore *Gobiusculus flavescens*. J Fish Biol 50:926–938

Utne-Palm AC (1999) The effect of prey mobility, prey contrast, turbidity and spectral composition on the reaction distance of *Gobiusculus flavescens* to its planktonic prey. J Fish Biol 54:1244–1258

Utne-Palm AC (2000) Prey visibility, activity, size and catchability's (evasiveness) influence on *Gobiusculus flavescens* prey choice. Sarsia 85:157–165

Utne-Palm AC, Bowmaker JK (2006) Spectral sensitivity of the two-spotted goby (*Gobiusculus flavescens*): a physiological and behavioural study. J Exp Biol 209:2034–2041

Villarreal CA, Thorpe JE, Miles MS (1988) Influence of photoperiod on growth changes in juvenile Atlantic salmon, *Salrno salar* L. J Fish Biol 33:15–30

Vinyard GL, O'Brien WJ (1976) Effects of light and turbidity on the reaction distance of bluegill (*Lepomis macrochirus*). J Fish Res Board Can 33:2845–2849

Ware DM (1971) Predation by rainbow trout (*Salmo gairdneri*): the effect of experience. J Fish Res Board Can 28:1847–1852

Webster DR, Weissburg MJ (2001) Chemosensory guidance cues in a turbulent chemical plume. Limnol Oceanogr 46:1034–1047

Wiseberg SB, Whalen R, Lotrich VA (1981) Tidal and diurnal influence on food consumption of a salt marsh killifish *Fundulus heteroclitus*. Mar Biol 61:243–246

Wright DJ, O'Brien WJ (1982) Differential location of Chaoborus larvae and Daphnia by: the importance of motion and visible size. Am Midl Nat 108:68–73

Yamaguchi Y, Nonoda T, Kobayashi H, Izawa K, Jinno T, Ishikura I, Uchida M, Tonogai M (1983) Effectiveness of artificial bait for obtaining higher hooking rate on bottom set long-line fishing. Bull Jpn Soc Fish Oceanogr 42:1819–1824

Yamashita S, Yamada T, Hara TJ (2006) Gustatory responses to feeding- and non-feeding-stimulant chemicals, with an emphasis on amino acids, in rainbow trout. J Fish Biol 68:783–800

Zarubin M, Belkin S, Ionescu M, Genin A (2012) Bacterial bioluminescence as a lure for marine zooplankton and fish. Proc Nat Acad Sci 109:853–857

Zeiske E, Theisen B, Breucker H (1992) Structure, development, and evolutionary aspects of the peripheral olfactory system. In: Hara TJ (ed) Fish chemoreception. Chapman & Hall, London, pp 13–39